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ON A NEW INDEX OF HOST SPECIFICITY

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Summary « On a new index of host specificity »

To facilitate consistent comparisons of host specificities among disparate taxa, a new index of host specificity is proposed. This index takes into account host range and host taxonomic rank, but not prevalence or intensity of infection. The central premise of this index is that a parasite lacking specificity at a higher taxonomic level should be considered to be less host specific than one lacking specificity at a lower taxonomic level. A ranking scheme is adopted that accommodates this notion. Host associations are ranked in order beginning with 1 for the most host specific scenario, corresponding to a taxon parasitizing 1 species, 1 genus, 1 family, 1 order, 1 class of host, and ending with a rank of 11,795,988,501, for the least host specific scenario, corresponding to a taxon parasitizing the greatest number of hosts allowed by this scheme (i.e., 1,000 species, 500 genera, 150 families, 75 orders, 5 classes). These unwieldy rank values are converted to more intuitive index values, which range from 1 to approximately 10, by taking the log (base 10) of the rank value. A Windows program to assist with the computation of rank and index value is available at http://darwin.eeb.uconn.edu/specificity/specificity.html. Standardization of the terminology applied to host specificity is proposed using this new index

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as follows : *oioxeny* for parasites restricted to a single species of host (index value of 0), *mesostenoxeny* for parasites restricted to species in a single genus of hosts (index values between 0 and 3.0004), *metastenoxeny* for parasites restricted to a single family of hosts (index values greater than or equal to 3.0004 and less than 5.574322), and *euryxeny* for parasitizing host in greater than one family (index values equal to or greater than 5.574322). In addition, ranges of index values are suggested to delimit the ecological terms 'specialist' and 'generalist.' The potential utility of the index was examined using data gathered from the literature on host ranges for approximately 700 species representing five phyla of parasitic organisms, and six common generalizations about host specificity.

Key words

Specificity Index - Host Range - Specialist - Generalist - Oioxeny - Stenoxeny - Euryxeny

Résumé « Sur un nouvel indice de spécificité pour l'hôte »

Afin de faciliter des comparaisons cohérentes des spécificités pour l'hôte entre des taxons quelconques, un nouvel index de spécificité pour l'hôte est proposé. Cet index prend en compte le spectre d'hôtes et la taxonomie de l'hôte mais ni la prévalence ni l'intensité de l'infestation. Le principe autour duquel s'articule cet index est qu'un parasite dépourvu de spécificité à un niveau taxonomique élevé doit être considéré comme moins spécifique pour l'hôte qu'un parasite dépourvu de spécificité à un niveau taxonomique moins élevé. Un système de rangs est adopté pour répondre à cette notion.

Les associations d'hôtes sont rangées dans un ordre qui commence à 1 pour le scénario le plus spécifique, correspondant à un taxon qui parasite 1 espèce, 1 genre, 1 famille, 1 ordre, 1 classe d'hôte, et se termine à la valeur 11.795.988.501 pour le scénario le moins spécifique, correspondant à un taxon qui parasiterait le plus grand nombre d'hôtes permis par le système (à savoir 1000 espèces, 500 genres, 150 familles, 75 ordres, 5 classes). Ces valeurs de rang peu maniables sont converties en valeurs d'indice plus intuitives qui vont de 1 à approximativement 10 en prenant le logarithme de base 10 de la valeur de rang. Un programme sur Windows pour le calcul du rang et de l'indice est disponible à http://darwin.eeb.uconn.edu/specificity/specificity.html.

Une standardisation de la terminologie appliquée à la spécificité d'hôte est proposée en utilisant le nouvel indice comme suit : *oioxénie* pour les parasites dont le spectre est réduit à une seule espèce d'hôte (indice = 0), *mésosténoxénie* pour les parasites se limitant aux espèces d'un même genre d'hôtes (indice entre 0 et 3,0004), *métasténoxénie* pour les parasites n'exploitant que les membres d'une même famille d'hôtes (indice entre 3,0004 et 5,574322) et *euryxénie* pour les parasites se trouvant dans plus d'une famille d'hôtes (indice égal ou supérieur à 5,574322). Des intervalles des valeurs de l'indice sont suggérées pour délimiter les termes écologiques de « spécialiste » ou « généraliste ». L'utilité potentielle de l'indice a été testée en utilisant des données prises dans la littérature sur des spectres d'hôtes d'environ 700 espèces représentant cinq phylums de parasites, et six généralisations habituelles relatives à la spécificité.

Mots-clés

Spécificité d'hôte - Indice de spécificité - Spectre d'hôtes - Spécialiste - Généraliste - Oioxénie - Sténoxénie - Euryxénie

The concept of host specificity is among the most intriguing aspects of Parasitology. The literature exploring the various facets of this concept is extensive. Generalizations about the specificities of parasite groups abound in the literature (e.g., Rohde, 1978 ; Noble *et al.*, 1989 ; Holmes, 1990 ; Poulin, 1992 ; Sasal *et al.*, 1999). Within the last 50 years alone, two major symposia have been held to address this topic ; both of these resulted in interesting compilations of papers (Baer, 1957 ; Chabaud, 1982). By now it is apparent that all parasites exhibit some degree of specificity for the kinds of organisms they parasitize at any single life-stage. It is also apparent that the extensive diversity of known parasites collectively exhibits a wide spectrum of host associations (e.g., Rohde, 1978 ; Noble *et al.*, 1989 ; Poulin, 1992 ; Combes, 2001). Despite the continuous nature of this spectrum of host associations, the utility of distinguishing between parasites falling at either of its extremes is widely recognized. However, neither the specific boundaries of the extremes, nor the terminology for characterizing host specificity at either extreme are universally agreed upon.

At one end of this spectrum are taxa that parasitize only a single species of host. A number of terms have been used to describe species exhibiting such restricted host specificity. Sandground (1929) considered such taxa to be 'monoxenous,' but noted that this term could also be applied to parasites associated with several very closely related hosts. Marshall (1981) restricted use of 'monoxeny' to parasites known only from one host species. Hargis (1957) referred to such taxa as exhibiting 'species-specificity.' Ludwig (1982) used the term 'stenohospitalic.' Euzet and Combes (1980) suggested the term 'oioxenous' for parasites restricted to one species of host ; Lambert (1982) followed suit. Such taxa have also been described as 'host-specific' by many authors (e.g., Moss & Wojcik, 1978), and as 'specialists' in much of the ecological literature (e.g., Dusek *et al.*, 1998 ; Sasal *et al.*, 1999). The latter two terms have also been applied to parasite species exhibiting slightly more relaxed host specificities ; most commonly, those parasitizing a suite of closely related hosts (e.g., Esch & Fernandez, 1993). Cumming (1998 ; pg. 380) very precisely defined specialists as « those species that have been collected more than ten times and where 90% or more of collections are from a single taxon. » Some of the problems associated with the lack of precision of terms used to characterize 'species specificity' in specific taxonomic groups have been articulated by others (e.g., Williams, 1986).

The boundary at the other end of the spectrum is less well defined. A diversity of terms has been proposed to describe a lack of specificity, and the exact concept to which each of these terms has been applied has also varied. Parasites designated as lacking in specificity have included : species parasitizing two or more closely related species of hosts (e.g., Ludwig, 1982), species parasitizing many species of hosts (e.g., Sandground, 1929), and species parasitizing many distantly related species of hosts (e.g., Esch & Fernandez, 1993). Sandground (1929) referred to taxa parasitizing a diversity of hosts as 'polyxenous.' Marshall (1981) more precisely defined 'polyxenous' taxa as those parasitizing more than one family of host. Euzet and Combes (1980) proposed the term 'euryxenous' for species parasitizing a number of distantly related hosts. Hoogstraal and Aeschlimann (1982) developed an elaborate scheme of terms that incorporated specificity of both immature and adult tick stages ; taxa exhibiting the least amount of host specificity (i.e., in which both adults and immatures « are both catholic in host acceptability » [p. 157]), were referred to as 'nonparticular' or 'telotropic.' Ludwig (1982) termed species exhibiting wide host specificity 'euryhospitalic.' Among ecologists, such taxa are most commonly referred to as 'generalists.' However, application of the latter term has also varied. To some (e.g., Dusek *et al.*, 1998), a generalist is a parasite occurring on several host species ; to others (e.g., see Esch & Fernandez, 1993), it is a parasite associated with a broad range of unrelated host taxa. Cumming (1998) very precisely defined generalists as any species collected from greater than 50 species of host.

Many authors have sought to recognize one or more categories of specificity for parasites exhibiting host associations falling between the two extremes described above. For example, Sandground (1929) referred to parasites whose potential hosts are few in number as 'oligoxenous.' A category for parasites restricted to a closely related group of hosts is widely recognized. But, again, a number of different terms have been applied. For example, a natural group of monogeneans parasitizing a natural group of fish species was described as exhibiting 'supraspecific specificity' by Hargis (1957). Hoogstraal and Aeschlimann (1982) proposed the terms 'ditropic-A,' 'ditropic-B,' 'telotropic-moderate,' etc. for such taxa, depending on how taxon-limited the specificity exhibited by the parasite was. Euzet and Combes (1980) proposed the term 'stenoxenous' for parasites restricted to a small group of related hosts, usually the same genus or family. Marshall (1981) recognized two categories of moderately host-specific taxa ; he termed parasites associated with two or more congeners 'oligoxenous' and those associated with two or more genera in the same family of host 'pleioxenous.' Llewellyn (1982) advocated a somewhat different approach that emphasized degree of host relationship over number of hosts. He proposed the term 'phylogenetic specificity' for related parasites occuring on related hosts and 'ecological specificity' for parasites occurring on unrelated hosts, sharing a common habitat.

Although some of this terminology has subsequently been adopted by other authors (e.g., Lambert, 1982 followed Euzet & Combes, 1980), no set of terms or concepts has been universally accepted. It remains commonplace for authors to characterize parasites as exhibiting, for example, « little host specificity » (Steinlein *et al.*, 2001, p. 611), « very broad host specificity » (Podlipaev, 2001, p. 648), or « a rather high level of host specificity » (Telford *et al.*, 2001, p. 904). Clearly these types of characterizations limit the power of comparisons across taxa.

A metric or index of host specificity would greatly facilitate precise, reproducible specificity comparisons. However, the quantitative measures available are surprisingly few in number. In addition, as noted by Lymbery (1989), there is variation in the meaning intended by different authors using the term 'host specificity.' In much of the ecological literature this term is used in the sense of 'host preference' or 'host specificity' sensu Lymbery (1989). The available indices primarily reflect this concept of 'host specificity.' Rohde (1980) evaluated three host specificity indices and their potential applications. The first of these relies to a large extent on intensities of infection. The second relies heavily on prevalence of infection. The third is based on probability theory and relies to some extent on number of host species infected relative to the number of host species examined, although one of the variations of this index accommodates host range. Price (1980) suggested that an index of specificity for a higher taxon, such as family, might be calculated as the percent of species in that category utilizing only a single host. May's (1990) method for calculating effective specialization is considered by some (e.g., Mawdsley & Stork, 1997) to be a measure of host specificity. However, that metric was developed primarily in response to the interest in determining accurate estimates of global arthropod diversity (e.g., May, 1979 ; Erwin, 1982 ; Mawdsley & Stork, 1997 ; Ødegaard, 2000) and, as a consequence, is a host-centric rather than parasite-centric metric. This is also true of the index described by Marshall (1981). Alternatively, Poulin (1992, 1997) used number of known host species (or 'host range' sensu

Lymbery, 1989) to estimate host specificity at the species level. To estimate host specificity for higher taxa, Poulin (1992) used percentage of parasite species in the taxon known from only a single host, and mean number of known host species per parasite species. With the exception of the metrics utilized by Poulin and one version of Rohde's third index, all of the above indices are essentially measures of either host preference, or host specificity in its more ecological sense (i.e., sensu Lymbery, 1989). None of the above metrics take host relationships into account.

It is 'host specificity' in the sense of 'host range' that is of interest to us here. However, we prefer a slightly more comprehensive concept combining information on host range (i.e., number of host species parasitized) and the phylogenetic limits of this host range. Because none of the above indices were designed to account for any element of host relationships, all of these metrics fail to distinguish between the specificity of a taxon parasitizing a group of related hosts from that of a taxon parasitizing a suite of more distantly related hosts, and thus are inappropriate indices of the concept of host specificity we are striving to measure here.

The development of an index of host specificity that incorporates data on both number and basic taxonomic position of hosts is the subject of this chapter. This seemed an appropriate endeavor to undertake in a book honoring Professor Louis Euzet, for Professor Euzet has not only contributed to the formalization of the terminology of host specificity, but has also contributed enormously to the taxonomy and systematics of two of the most host-specific parasite groups known. This index was designed to measure host specificity sensu Euzet and Combes (1980) rather than, for example, host specificity as defined by Lymbery (1989). Thus, it does not take into account prevalence or intensity of infection. In order to distinguish the index described here from other specificity indices, we have adopted the abbreviation *HS*.

Index of Host Specificity (*HS*)

The issue of how best to incorporate basic host phylogenetic information was perhaps the biggest challenge in the development of the index. Although a strictly tree-based system might reflect the phylogenetic components of the hosts most effectively, it would only be useful for comparing those parasites for which well-corroborated host phylogenies were available and only for comparing parasites in which the tree of host relationships for one was a subset of the tree of host relationships for the other. In addition, if the comparisons were to be meaningful, the host trees utilized would need to include all species in each host group, because, barring extensive polytomy, the number of nodes in a tree is generally correlated with number of species in the tree and thus missing taxa would significantly affect the assessment of relative phylogenetic specificity. As a result, a tree-based index would also be severely biased by differences in the extent of extinction among host groups because host range information is generally available only for extant taxa. However, even if fully resolved trees of all host taxa were available, the issue of which nodes to consider equivalent when comparing trees generated for parasites of host taxa consisting of different numbers of included species would be difficult to resolve. In short, although a tree-based index might be useful for analyses of co-evolution, it is not clear that such a system could be used to compare host specificities of distantly related taxa.

Instead, the Linnaean hierarchy from species through class, was adopted as the criterion to be used to represent host relationships. This hierarchy was incorporated by requiring that each parasite be scored for the number of species, genera, families, orders and classes of taxa it parasitizes. Taxonomic categories above class were not included because examination of the host associations of a disparate suite of 700 parasite taxa (see Appendix I) failed to identify a single taxon parasitizing more than 1 phylum (or kingdom) at any single life-stage ; although, several taxa parasitizing more than a single class of hosts were identified. If taxa parasitizing more than a single phylum or kingdom, at the same life-stage, exist, they are rare and are best treated on an individual basis when they arise. It should be noted, however, that the trichodinid ciliates may prove to be just such an exception (Van As & Basson, 1987). In basing our index of specificity on the rank at which specificity is detected, we are implicitly assuming that taxonomic categories across host groups are comparable, that higher taxa represent monophyletic units, and that phyletic distance is a more important component of specificity than the number of species parasitized. It was our hope that at least discrepancies in taxonomic rank among disparate host taxa would be buffered by our focus on major taxonomic categories only. There seemed little reason to believe that differences in classification among host groups were major enough to transcend the basic major taxonomic categories of classification. Thus, for example, even if genera of fish and mammals are not quite equivalent, they are not so different that a genus of fish is the equivalent of a family of mammals. Our index is a move in the direction of a tree-based index of specificity that, we hope, represents a useful compromise between incorporating relevant phylogenetic information on hosts and allowing broad comparisons among parasites infecting distantly related host taxa.

One of the primary features we wished the index to reflect was the premise that a parasite lacking specificity at a higher taxonomic level (e.g., a parasite hosted by two genera) should be considered less host specific than one lacking specificity at a relatively lower taxonomic level (e.g., a parasite hosted by any number of species in a single genus). The higher the taxonomic category at which this lack of specificity is exhibited, the less host specific the taxon. A basic ranking scheme was adopted that would reflect this premise. In this scheme, all possible numbers of hosts in each taxonomic category are uniquely ranked, in sequence, beginning with 1 species in 1 genus in 1 family in 1 order in 1 class of host (i.e., the most host specific scenario) and ending with the maximum number of species, genera, families, orders and classes (i.e., the least host specific scenario).

It is easiest to understand how a parasite species is assigned a unique rank by describing how data on host ranges is used to determine the rank assigned to a species. Let S, G, F, O, and C be the number of species, genera, families, orders, and classes, respectively, in which a particular taxon occurs. We can then represent the host distribution of any parasite species as a decimalized index, namely C.O.F.G.S. We can then list all possible decimalized indices by enumerating all combinations of S, G, F, O, and C, provided that we specify the maximum number of taxa a parasite can infect at any hierarchical level. Let S_{Max}, G_{Max}, F_{Max}, O_{Max}, and C_{Max} be those maximum numbers. We can then sort the decimalized indices from most specific (1.1.1.1.1) to least specific ($C_{Max}.O_{Max}.F_{Max}.G_{Max}.S_{Max}$) by sorting first on the number of classes in which a species is found, then on the number of orders, then on the number of families, then on the number of genera, then on the number of species. Any parasite species will have a unique position in this sorted list ranging from 1 for the most specific taxa to some very large number that depends on S_{Max}, G_{Max}, F_{Max}, O_{Max}, and C_{Max} for the least specific. That unique position is the rank assigned to a parasite species. The C++ code for a more computationally efficient algorithm is included as Appendix II.

However, before the total number of possible ranks could be determined, it was necessary to determine the maximum number of host taxa to allow at each of the five taxonomic levels (i.e., S_{Max}, G_{Max}, F_{Max}, O_{Max}, and C_{Max}). Of primary concern was that these values be set large enough to accommodate the specificity exhibited by even the least host specific parasite system ; the larger the maximum values allowed, the more likely this is to be the case. However, the larger these values, the greater the number of possible ranks, and the more unwieldy the index. We initially considered setting these numbers to the total number of known taxa in each category. So, for example, these values might be set to 2 million species, 100,000 genera, etc. However, this strategy results in an outrageously large number of ranks (possibly as many as 10^{15}), and, given that no parasite taxon is known to parasitize all species, this strategy was determined to be unnecessarily conservative. It seemed more appropriate to assign these maximum values following examination of published host data. Thus, data from the literature were assembled on numbers of species, genera, families, orders, and classes parasitized by each of 700 species representing a diversity of host/parasite systems, at least some of which are generally considered to be notoriously nonhost-specific. These data are summarized in Appendix I.

One additional consideration played a role in the determination of these maximum values. Although host specificity is most commonly investigated at the level of parasite species, it has been addressed at higher taxonomic categories such genus, family, or order (e.g., Hargis, 1957 ; Moss, 1979 ; Rohde, 1979 ; Marshall, 1981 ; Kim, 1982 ; Ludwig, 1982 ; Cumming, 1998 ; Caira & Jensen, 2001). If the index were to have utility for addressing questions relating to higher taxonomic categories of parasites, the maximum values would need to be sufficiently high so as to accommodate all host taxa at each taxonomic category parasitized by, for example all species in a genus, or all species in a family of parasite. The maximum numbers of host taxa parasitized by any single species of parasite in each of the five taxonomic categories seen in Appendix I are : 58 species, 37 genera, 17 families, 12 orders and 2 classes. The maximum numbers of host taxa parasitized by any single genus of parasite in each of the five taxonomic categories seen in Appendix I are : 100 species, 71 genera, 45 families, 18 orders and 2 classes. The maximum numbers of host taxa parasitized by any single family of parasite in each of the 5 taxonomic categories seen in Appendix I are : 139 species, 97 genera, 55 families, 19 orders and 2 classes. Given that these data represent only a tiny fraction of all parasite taxa, and less host specific taxa are likely to exist, it seemed appropriate to set the maximum values substantially higher than any seen among these data. We chose maximum values of : 1,000 species, 500 genera, 150 families, 75 orders and 5 classes. These numbers result in a total number of 11,795,988,501 ranks. The highest rank represents the least host specific scenario allowed under this configuration and would be assigned to any taxon parasitizing 1,000 species, 500 genera, 150 families, 75 orders and 5 classes of hosts. So, a taxon parasitizing 1 species in 1 genus in 1 family in 1 order would receive the rank of 1. A taxon parasitizing 1,000 species in 500 genera in 100 families in 50 orders receive the rank of 11,795,988,501. Taxa exhibiting all other possible combinations of host associations receive ranks falling between these two values. For example, a taxon parasitizing 1,000 species in 1 genus in 1 family in 1 order in 1 class would receive a rank of 1,000. A taxon parasitizing 2 species in 2 genera in 1 family in 1 order in 1 class would receive a rank of 1001, etc. The corresponding decimalized index value for the most host specific parasite would be : 1.1.1.1.1 ; the decimalized index value for the least host specific parasite allowed by this system would be : 1000.500.150.75.5.

Unfortunately, the extensive range of the raw rank values and the complex representation of the decimalized index make them awkward to use and difficult to compare. Perhaps more importantly, the difference in specificity between a species that parasitizes only 1 species and one that parasitizes 2 species in 1 genus seems far greater to us than the difference between a species that parasitizes 10 species in 5 genera in 1 family and one that parasitizes, 11 species in 5 genera in 1 family. By taking the logarithm (base 10) of the raw rank value we change our metric from ranks of 1-11,795,988,501, to an index of 0 to ~10 (or more precisely, 10.07173434). A taxon parasitizing 1 species in 1 genus in 1 family in 1 order in 1 class (i.e., with a rank of 1) would be assigned an index value of log10(1), or 0. A taxon parasitizing 1,000 species in 500 genera in 150 families in 75 orders in 5 classes (i.e. with the rank of 11,795,988,501) would be assigned the index value of log10 (11,795,988,501), or 10.07173434. The lower the index value, the higher the degree of specificity exhibited by a taxon.

The conversion to a log10 scale has several consequences that are important to note. Perhaps most importantly, this conversion results in the index being of much finer scale at its lower values. Thus, for example, taxa parasitizing hosts in 1 order in 1 class and any number of genera or species (below 500 and 1.000, respectively) will be assigned index values between 0 and 7.65957204. Whereas, those parasitizing any combination of numbers of taxonomic categories in 2 to 75 orders in 2 to 5 classes will receive values between 7.65957204 and 10.0717343. This attribute reflects our decision to emphasize proportional differences in degree of specificity rather than absolute differences in specificity rank. The detailed comparison of taxa exhibiting greater specificities (lower indices) may be more interesting than the probing of those with lesser specificities (higher indices). An appreciation for the degrees of host specificity represented by the various index values can be obtained by examining Table I, in which the host associations represented by each whole number index value are presented. In order to illustrate the variation in scale noted above, index values of 7.5, 8.5, and 9.5 are also included.

To facilitate computation of the rank and its corresponding index value from the number of host species, genera, families, orders and classes parasitized, a Windows program (including source code in C++) is available from http://darwin.eeb.uconn.edu/specificity/specificity.html. The program uses our choice of values for maximum number of species, genera, families, orders and classes by default (i.e., 1.000, 500, 100, 75, and 5, respectively), but the algorithm is completely general (see Appendix II). Although users can modify the default values of these maximums by selecting appropriate options, we encourage users to resist changing the default values unless they encounter a taxon that exceeds the maximum values described above. Changes in these default values will require recalculation of all index values

	HOSTS						
	No. species	No. genera	No. families	No. orders	No. classes	Rank	Index (*HS*)
	1	1	1	1	1	1	0.00000000
	10	1	1	1	1	10	1.00000000
	100	1	1	1	1	100	2.00000000
	1000	1	1	1	1	1000	3.00000000
	55	11	1	1	1	10000	4.00000000
	565	106	1	1	1	100000	5.00000000
	455	297	3	1	1	1000000	6.00000000
	877	283	28	1	1	10000000	7.00000000
	778	114	97	1	1	31622777	7.50000001
	944	41	28	3	1	100000000	8.00000000
	906	96	20	8	1	316227766	8.50000000
	325	171	41	25	1	1000000000	9.00000000
	633	178	122	18	2	3162277660	9.50000000
	573	120	38	16	5	10000000000	10.00000000
	1000	500	150	75	5	11795988501	10.07173434
Host specificity categories							
oioxeny	1	1	1	1	1	1	0.00000000
lower boundary of mesostenoxeny	2	1	1	1	1	2	0.30103000
lower boundary of metastenoxeny	2	2	1	1	1	1001	3.00043408
lower boundary of euryxeny	2	2	2	1	1	375251	5.57432186

Table 1. Host specificity index landmarks.

obtained using our original default values if comparisons are to be made across datasets. We recommend that investigators using this index present at least the rank and index value for each parasite taxon investigated. However, it would be even more useful to present the number of species, genera, families, orders and classes of hosts in each case. This could be done in a concise manner using the decimalized index scheme described above. These host data are necessary if the maximum value of any taxonomic category is altered and recalibration of the index is required. Although these values can be retrieved from the raw rank, the retrieval process is very tedious.

So as to increase the precision of the terminology used to characterize the host associations of parasites (Combes, 2001), we suggest that quantitative definitions based on the index developed here would be very appropriate. We propose a system that allows the basic terms suggested by Euzet and Combes (1980) to be applied with only slight modification. We prefer these terms over those of, for example, Sandground (1929) and Marshall (1981), because the terms used by the latter authors have a history of alternate usage associated with the number of hosts parasitized over the course of the life cycle of a parasite (i.e., monoxenous = one host ; polyxenous = greater than one host). We think it advisable not to confuse the issue of number of hosts in the complete life-cycle of a taxon with number of hosts parasitized by one life-stage of a taxon. We propose the following :

1) An *oioxenous* taxon is restricted to a single species of host and has an index value of 0.

2) Two subcategories of stenoxenous specificity that reflect the two intermediate categories of specificity of Marshall (1981) should be recognized :

a) A *mesostenoxenous* taxon parasitizes greater than 1 species of host, but is restricted to a single genus of host ; such taxa have index values greater than 0 and less than 3.000434077. Note that because the highest possible index value of a parasite restricted to a single genus of host is 3.00000000 (i.e, 1.000 species, 1 genus, 1 family, 1 order and 1 class), it is necessary to calculate and present index values to at least four decimal places if the difference between this and the next rank is to be detected.

b) A *metastenoxenous* taxon parasitizes more than one genus of host, but is restricted to a single family of host ; such taxa have index values greater than or equal 3.00043400 and less than 5.574321858. Once again, because the highest possible index value of a parasite restricted to a single family of host is 5.574320701 (i.e. 1,000 species, 500 genera, 1 family, 1 order and 1 class), it is necessary to calculate and present index values to at least 6 decimal places if the difference between this and the next rank is to be detected.

3) A *euryxenous* taxon parasitizes more than one family of host ; such taxa have index values equal to or greater than 5.574322.

Because ecologists so commonly use the terms 'specialist' and 'generalist' to describe host associations, we would also like to suggest index values to delimit these terms. Although, as noted above, there is not complete consensus among ecologists as to the boundary between these two terms, we suggest that taxa exhibiting oioxeny or mesostenoxeny should be considered specialists and those exhibiting metastenoxeny or euryxeny should be considered generalists. Thus, specialists would be taxa with index values less than 3.0004 and generalists would those with index values of 3.0004 or greater.

Exploring the Index

The index and the data provided in Appendix I are used below to explore several of the major generalizations about parasite specificity that exist in the literature. This allows us to demonstrate the utility of the index. In addition, we attempt to gain additional insight into patterns of specificity by comparing an index value calculated from a rank generated for a higher parasite taxon with an index value that represents a mean of the index values of the species associated with that higher parasite taxon.

The host association data provided in Appendix I were obtained from a variety of sources. While it was beyond the scope of this work to attempt to verify the specific identities of the host or parasite taxa, we have attempted to standardize the higher categories to which each of the host species of record was assigned. The classification schemes followed were : Fishbase

(2002) for fishes, Nowak (1991) for mammals, Clements (2000) for birds, and Stevens (2001) for plants. The host data presented here include natural infections only ; data from experimental infections were excluded. This is particularly relevant to the mermithid nematodes. Hosts suspected to be the result of accidental infections were also excluded. In general, the hosts presented are only those utilized by the adult parasite.

The 700 species in Appendix I were chosen to represent the major groups of metazoan parasites, while also representing a diversity of endoparasites and ectoparasites, and a number of distinct host groups. As noted above, a special point was made to include groups generally considered to be lacking in host specificity. This was the primary factor that led to the inclusion of the mycorrhizal fungi. Groups generally perceived to be very host specific are also represented. Whenever possible, data were collected for multiple species in multiple genera of parasites in a family so as to allow comparisons of index calculations for parasites of different taxonomic levels, as well as to allow these numbers to be compared to mean index calculations at these levels. In deference to the taxonomic interests of Professor Euzet, there is a slight emphasis on monogeneans.

The overall organization of Appendix I is by parasite phylum. Data provided include parasite family, genus and species identity. For each species of parasite the number of species, genera, families, orders and classes of hosts parasitized, the source of these data, the rank, and the index value assigned to each species based on these associations are provided. The endoparasites consist of : 1) Nematoda (12 mermithids, 1 diplogasterid, 4 steinernematids, 2 heterorhabditids, 1 neotylenchid, 1 allantonematid, and 26 cystidicolids), 2) Digenea (49 hemiurds, 49 leptocreadiids, 18 allocreadiids), 3) Cestoda (3 cephalochlamydids, 8 litobothriids, and 35 onchobothriids), and 4) Acanthocephala (19 neoechinorhynchids). The ectoparasites consist of : 1) Monogenea (34 gyrodactylids, 11 dactylogyrids, 39 monocotylids, 2 capsalids, 4 hexabothriids, 5 mazocreadiids, 4 discocotylids, 5 diclydophorids, 15 microcotylids, 8 gastrocotylids, 2) Copepoda (79 caligids and 28 pandarids), 3) Acari : 'ticks' (19 ixodids), 4) Acari : 'mites' (114 harpyrhynchids), 5) Siphonaptera (53 ceratophyllids), and 6) Mallophaga (8 phyllopterids). In addition, 46 mycorrhizal fungi of the order Aphyllophorales were included.

I. Parasite species indices (HS_S)

Index values for individual species (designated) are plotted in Figure 1. Shaded regions indicate the recommended index ranges for oioxenous, mesostenoxenous, metastenoxenous, and euryxenous taxa, as described above. Several basic trends are apparent from these data. For example, species in some groups, such as the onchobothriid tapeworms and many of the monogeneans, all exhibit similar degrees of specificity. These species

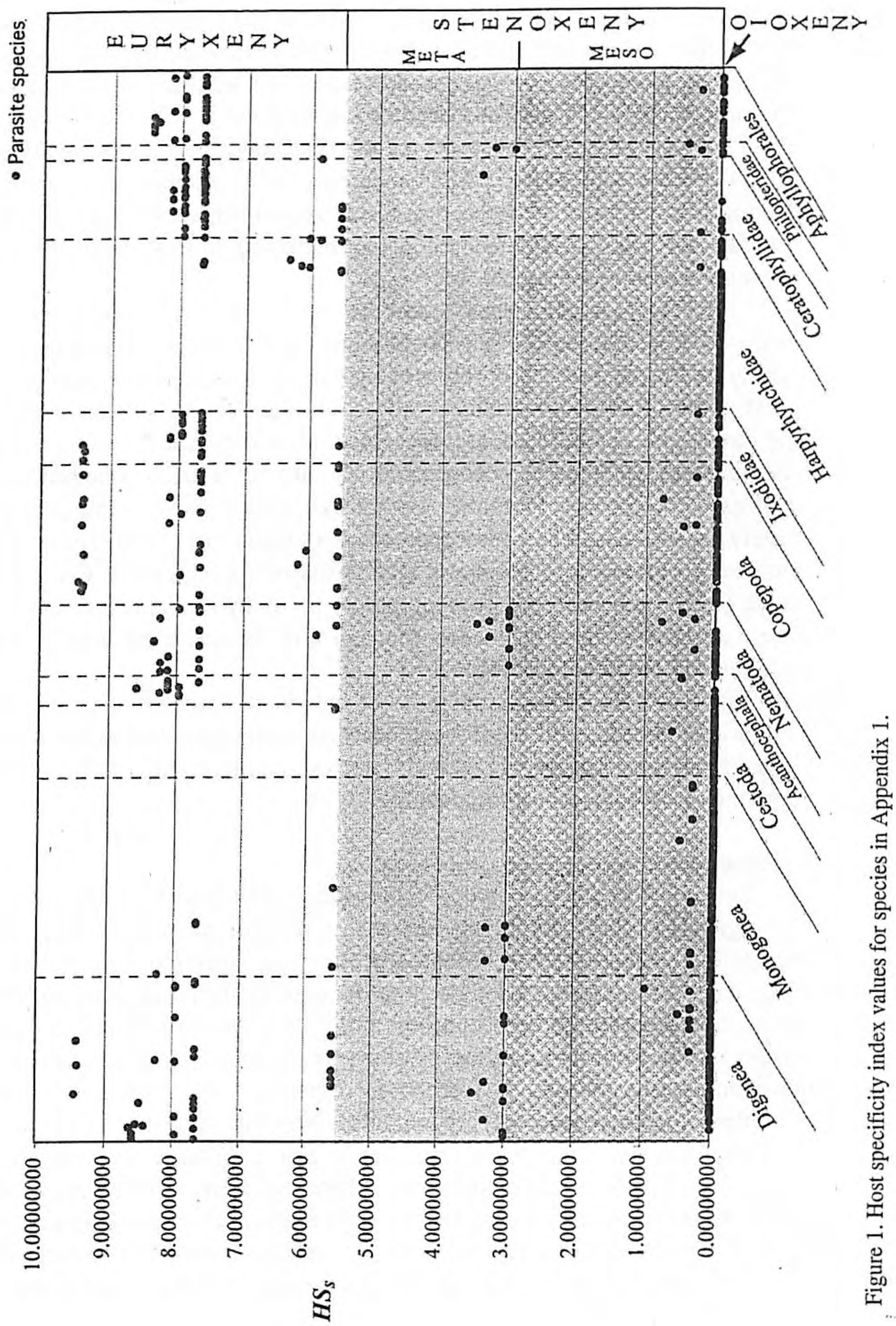

Figure 1. Host specificity index values for species in Appendix 1.

tend to be very host specific ; most are oioxenous (i.e., have index values of 0). However, there are other groups, such as the copepods and the digeneans, that collectively include species with a wide diversity of host specificities. Both of these groups include many species that are oioxenous, but many more species that are among the most euryxenous of the species included in this study. Both groups also include a number of stenoxenous species. However, whereas the digeneans include both mesostenoxenous and metastenoxenous species, the non-oioxenous copepods are entirely metastenoxenous. The mycorrhizal fungi are interesting in that species are either oioxenous or euryxenous.

Oioxenous specificity was exhibited by one or more species in all but 4 of the 31 families in the 5 phyla examined. In the higher parasite taxa (i.e., family or above) that are represented by 8 or more species in Appendix I, the greatest numbers of oioxenous taxa were seen among the Platyhelminthes in the monogenean families Dactylogyridae, Monocotylidae, and Microcotylidae, and in the tapeworm families Onchobothriidae and Litobothriidae, as well as in the arthropod family Harpyrhynchidae ; in each case, approximately 90% or greater of the species had an index value of 0. The smallest number of oioxenous species was seen in the arthropod families Ceratophylliidae (fleas) and Ixodidae (ticks), and in the Platyhelminthes, in the digenean family Allocreadiidae. Less than 30% of the species in each of these families had index values of 0.

The least host specific species were caligid and pandarid copepods, and hemiurid digeneans. Of the 12 species that exhibited index values greater than 9.3, 5 were caligid copepods, 4 were pandarid copepods, and the remaining 3 were hemiurid digeneans.

II. Generic indices

Two types of generic index values can be obtained from this system. Mean generic values can be calculated by averaging the index values of all species in a genus (HS_s). Alternatively, an index value for the genus itself (HS_g) can be generated by determining the rank for the genus from the number of host species, genera, families, orders and classes parasitized by all species in the genus. Both of these values are presented in Table II for the 79 non-monotypic (metazoan) genera from Appendix I for which data on specific identifications of hosts were available. Note that these two index values are conspicuously different for a number of genera. Instances in which these values are similar are indicative of substantial host overlap among the species in the genus. For example, in the ceratophyllid flea genus *Monopsyllus*, the mean generic index value (HS_s) for the six included species was 7.89 ± 0.08, and the index value for the genus (HS_g) was 8.14. Indeed, the 80

PARASITES				HOSTS							
Family	n*	Genus	Mean Generic Index ($\overline{HS}\ s$)	No. species	No. genera	No. families	No. orders	No. classes	Rank	Generic Index ($HS\ g$)	Generic In[dex] Ratio ($\overline{HS}s$ /HS
ALLOCREADIIDAE	4	*Bunodera*	6.80520758	39	28	12	9	1	355973905	8.55141816	0.7
	12	*Crepidostomum*	4.60066378	100	41	20	15	2	3011437755	9.47877389	0.4
HEMIURIDAE	4	*Aponurus*	1.91489301	4	4	4	3	1	90953349	7.95881869	0.2
	3	*Brachyphallus*	6.38497096	20	16	11	8	1	312908095	8.49541680	0.7
	4	*Derogenes*	4.27683193	50	28	16	10	2	2803855722	9.44775566	0.4
	3	*Dinosma*	3.85839706	5	4	4	2	1	45665799	7.65959106	0.5
	6	*Dinurus*	2.40827895	7	7	4	1	1	1125740	6.05143810	0.3
	5	*Ectenurus*	1.11486437	4	4	3	1	1	750499	5.87535012	0.1
	7	*Genolinea*	4.63702690	29	24	13	6	1	227158274	8.35632856	0.5
	4	*Gonocerca*	1.91489539	4	3	2	2	1	45664801	7.65958157	0.2
	2	*Gonocercella*	0.00000000	2	2	2	2	1	45663801	7.65957206	0.0
	4	*Hemiurus*	2.35496561	20	15	8	6	2	2629434956	9.41986243	0.2
LEPOCREADIIDAE	2	*Dihemistophenus*	0.00000000	1	1	1	1	1	1	0.00000000	N
	2	*Labifer*	0.00000000	2	2	2	1	1	375251	5.57432186	0.0
	12	*Lepidapedon*	1.30370611	17	11	6	4	1	136615131	8.13549880	0.1
	8	*Lepocreadium*	0.00000000	5	5	5	3	1	91697855	7.96235918	0.0
	4	*Neolepidapedon*	0.31381813	13	3	3	2	1	46038061	7.66311702	0.0
	8	*Opechona*	3.90503962	21	8	8	6	1	225316034	8.35279210	0.4
GYRODACTYLIDAE	35	*Gyrodactylus*	1.30460080	40	26	24	10	1	402589229	8.60486215	0.1
DACTYLOGYRIDAE	4	*Ancyrocephalus*	0.00000000	4	4	4	3	1	91325602	7.96059254	0.0
	2	*Pseudohalitrema*	0.00000000	2	2	2	1	1	375251	5.57432186	0.0
MONOCOTYLIDAE	4	*Calicotyle*	0.00000000	3	3	3	2	1	46038051	7.66311693	0.0
	3	*Decacotyle*	0.00000000	2	2	2	1	1	375251	5.57432186	0.0
	2	*Dendromonocotyle*	2.78716151	4	3	2	1	1	376251	5.57547766	0.4
	2	*Dionchus*	0.00000000	2	2	2	1	1	375251	5.57432186	0.0
	3	*Empruthotrema*	0.00000000	3	3	3	2	1	46038051	7.66311693	0.0
	4	*Heterocotyle*	0.00000000	3	3	2	1	1	376250	5.57547651	0.0
	3	*Merizocotyle*	0.00000000	3	3	3	1	1	749501	5.87477222	0.0
	6	*Monocotyle*	0.10034333	5	3	1	1	1	2002	3.30146407	0.0
	4	*Neoheterocotyle*	0.00000000	3	3	3	1	1	749501	5.87477222	0.0
	3	*Thaumatocotyle*	0.00000000	3	2	2	1	1	375252	5.57432302	0.0
HEXABOTHRIIDAE	2	*Squalonchocotyle*	0.00000000	2	2	2	2	1	45663801	7.65957206	0.0
MAZOCRAEIDAE	2	*Clupaeocotyle*	0.00000000	1	1	1	1	1	1	0.00000000	N
	2	*Mesocraeoides*	0.00000000	2	2	1	1	1	1001	3.00043408	0.0
DISCOCOTYLIDAE	3	*Tagia*	0.00000000	3	3	2	1	1	376250	5.57547651	0.0
DICLYDOPHORIDAE	4	*Choricotyle*	0.07525750	5	4	3	2	1	46039050	7.66312635	0.0
MICROCOTYLIDAE	3	*Axinoides*	0.00000000	2	1	1	1	1	2	0.30103000	0.0
	2	*Heteraxine*	0.00000000	2	2	2	1	1	375251	5.57432186	0.0
	7	*Microcotyle*	0.00000000	7	6	4	1	1	1124746	6.05105446	0.0
ONCHOBOTHRIIDAE	11	*Acanthobothrium*	0.00000000	5	3	3	2	1	46038053	7.66311695	0.0
	6	*Calliobothrium*	0.00000000	6	1	1	1	1	6	0.77815125	0.0
	9	*Pedibothrium*	0.00000000	4	4	2	1	1	377248	5.57662695	0.0
	6	*Platybothrium*	0.00000000	5	4	1	1	1	2999	3.47697647	0.0
LITOBOTHRIIDAE	8	*Litobothrium*	0.00000000	4	3	2	1	1	376251	5.57547766	0.0
PSEUDOPHYLLIDEA	2	*Cephalochlamys*	5.57432359	6	2	2	1	1	375255	5.57432649	1.0
NEOECHINORHYNCHIDAE	14	*Neoechinorhynchus*	5.78121852	56	36	15	10	2	2803503121	9.44770104	0.61
CYSTIDICOLIDAE	6	*Ascarophis*	4.00894550	30	17	12	7	1	270215379	8.43171006	0.4[illegible]
	4	*Cystidicola*	3.97918832	23	12	7	6	1	224951727	8.35208933	0.4[illegible]
	2	*Cystidicoloides*	4.06656281	16	9	5	5	1	180411685	8.25626466	0.4[illegible]
	3	*Salvelinema*	1.10077698	6	2	1	1	1	1005	3.00216606	0.3[illegible]
	7	*Spinitectus*	2.28809292	26	23	14	8	1	314004917	8.49693645	0.2[illegible]
HETERORHABDITIDAE	2	*Heterorhabditis*	0.00000000	2	2	1	1	1	1001	3.00043408	0.0
MERMITHIDAE	2	*Hydromermis*	4.52630004	11	9	3	1	1	755476	5.87822067	0.7
	2	*Isomermis*	2.03980766	9	2	1	1	1	1008	3.00346053	0.6
STEINERNEMATIDAE	4	*Neoaplectana*	6.05148415	17	15	10	3	1	93549132	7.97103976	0.7
CALIGIDAE	2	*Anuretes*	0.00000000	2	2	2	2	1	45663801	7.65957206	0.0
	41	*Caligus*	2.79633133	85	71	45	18	2	3139399080	9.49684653	0.2
	29	*Lepeophtheirus*	2.96787712	80	56	33	12	2	2893405801	9.46140935	0.31
	2	*Pupulina*	0.00000000	1	1	1	1	1	1	0.00000000	N
PANDARIDAE	2	*Demoleus*	3.82978603	2	2	2	2	1	45663801	7.65957206	0.5
	3	*Dinemoura*	5.21143516	7	6	5	2	1	46784552	7.67010248	0.67
	2	*Echthrogaleus*	8.53575874	8	8	7	3	2	2496552365	9.39734068	0.9
	5	*Nesippus*	2.23019176	8	5	3	2	1	46040049	7.66313578	0.29
	8	*Pandarus*	4.26642669	18	14	9	6	2	2629801246	9.41992293	0.45
	2	*Perissopus*	7.49709281	14	10	9	6	2	2629797288	9.41992227	0.79
IXODIDAE	3	*Dermacentor*	7.98077969	39	30	13	5	1	183366585	8.26332020	0.96
	15	*Ixodes*	5.22804675	42	28	13	5	1	183364645	8.26331560	0.63
CERATOPHYLLIDAE	2	*Amalaraeus*	7.81187831	20	14	6	3	1	92077049	7.96415139	0.98
	7	*Ceratophyllus*	3.02871424	17	14	6	3	1	92077046	7.96415138	0.38
	2	*Dactylophypsylla*	3.82978603	2	2	2	2	1	45663801	7.65957206	0.50
	3	*Malaraeus*	7.76169532	15	11	5	3	1	91703820	7.96238743	0.97
	9	*Megabothris*	6.51968398	55	29	10	4	1	138103918	8.14020600	0.80
	6	*Monopsyllus*	7.89157796	42	29	12	4	1	138833505	8.14249429	0.96
	3	*Opisocrostis*	7.75907477	14	10	5	3	1	91702829	7.96238273	0.97
	3	*Opisodasys*	7.76463049	17	11	6	3	1	92074082	7.96413740	0.97
	5	*Orchopeas*	6.88754953	38	26	9	4	1	137734696	8.13904335	0.84
	4	*Oropsylla*	7.89018204	33	23	9	3	1	93190714	7.96937264	0.99
	4	*Thrassis*	7.21441970	21	13	5	2	1	46791503	7.67016700	0.94
PHILOPTERIDAE	8	*Colingocola*	0.88495192	11	8	1	1	1	6983	3.84404204	0.23

Number of species in genus.

Table 2. Generic host specificity indices for non-monotypic metazoan genera from Appendix I. (N/A, [illegible] applicable).

PARASITES			HOSTS							
Family	n*	Mean Familial Index ($\overline{HSs}$)	No. species	No. genera	No. families	No. orders	No. classes	Rank	Familial Index (HSf)	Familial Index Ratio ($\overline{HSs}$ / HSf)
Allocreadiidae	18	5.05716660	117	53	24	16	1	648892693	8.81217288	0.573884179
Hemiuridae	50	2.76484776	100	65	34	13	2	2934983639	9.46760568	0.292032416
Leptocreadiidae	41	1.31744914	48	28	21	9	1	399208274	8.60119953	0.153170396
Gyrodactylidae	35	1.30460080	40	26	24	10	1	402589229	8.60486215	0.151612051
Dactylogyridae	12	0.00000000	12	12	10	6	2	2630165551	9.41998309	0
Monocotylidae	40	0.15440958	20	15	12	4	2	2542931784	9.40533471	0.016417233
Capsalidae	2	0.23856063	4	2	2	1	1	375253	5.57432417	0.042796332
Hexabothriidae	4	0.00000000	4	4	4	2	1	46411302	7.66662375	0
Mazocraeidae	5	0.00000000	2	2	1	1	1	1001	3.00043408	0
Discocotylidae	4	0.00000000	4	4	3	1	1	750499	5.87535012	0
Diclydophoridae	5	0.06020600	6	5	3	2	1	46040047	7.66313576	0.007856575
Microcotylidae	15	0.00000000	12	9	6	2	1	47157796	7.67355350	0
Gastrocotylidae	8	0.11288625	6	5	2	1	1	378246	5.57777434	0.020238583
Onchobothriidae	36	0.01672389	26	15	8	4	1	137356626	8.13784961	0.002055075
Litobothriidae	8	0.00000000	4	3	3	1	1	749502	5.87477280	0
Pseudophyllidea	3	3.71621573	6	3	3	1	1	749504	5.87477395	0.632571697
Neoechinorhynchidae	19	4.28495687	58	39	17	11	1	442069917	8.64549096	0.495629096
Cystidicolidae	26	2.70857567	77	49	29	16	2	3054748735	9.48497549	0.285564857
Heterorhabditidae	2	0.00000000	2	2	1	1	1	1001	3.00043408	0
Mermithidae	12	3.48708946	107	52	16	6	1	228269326	8.35844756	0.417193436
Steinernematidae	4	6.05148415	16	14	10	3	1	93548145	7.97103518	0.759184224
Caligidae	80	2.50897526	139	97	55	19	2	3181753992	9.50266660	0.264028548
Panderidae	28	4.14172096	28	21	14	8	2	2718114962	9.43426782	0.439008202
Ixodidae	19	5.80650774	65	34	16	5	1	184454509	8.26588928	0.702466189
Ceratophyllidae	53	6.49238163	116	44	15	4	1	139935024	8.14592643	0.797009608
Philopteridae	8	0.88495192	11	8	1	1	1	6983	3.84404204	0.230213901

* Number of species in family.

Table 3. Familial host specificity indices for non-monotypic metazoan families from Appendix I.

host records for these 6 flea species include only 42 unique host species. Instances in which these values differ are indicative of little host overlap among the species in the genus. For example, the mean generic index value (HS_S) for the four included species of diclydophorid monogeneans in the genus *Choricotyle* was 0.075, whereas the index value for this genus (HS_g) was 7.66. Examination of the host lists for these four species reveals no overlap in host species ; each parasitizes different species of teleosts, and collectively, these hosts belong to three different families of fishes. Calculation of the ratio of HS_S to HS_g provides a more convenient way to assess the proportion of the generic host range accounted for by the host range of an average species. A ratio of 1 indicates complete overlap in the host species parasitized by all species in the genus ; a ratio of 0 indicates no overlap in the host species parasitized by species in the genus. So for example, in the ceratophyllid flea genus *Monophyllus* this ratio (i.e.,HS_S /HS_g) is 0.97, whereas this ratio is 0.0098 for the diclydophorid monogenean genus *Choricotyle*.

III. Familial indices

Similarly, two types of familial index values can be obtained from this system. Mean familial values can be calculated by averaging the index values of all species in all genera in a family. Alternatively, an index value for the family (HS_f) itself can be determined by calculating a rank for the family from the number of host species, genera, families, orders and classes parasitized by all species in all genera in the family. Both of these values are presented in Table III for most of the non-monotypic (metazoan) families from Appendix I. Again, it is important to note that these two index values are conspicuously different for many families. In instances in which these values are similar, there exists much host overlap among the species in the family. In instances in which the index value for the family is conspicuously higher than the mean familial index value, there is little host overlap among the species in the family.

One of the advantages of this system is that mean index values can be calculated for essentially any suite of parasites so as to allow a diversity of comparisons to be made. We use such calculations below to examine several common generalizations about parasite specificity. In each case, the mean is followed by the standard error and the p value obtained from a Wilcoxon signed-rank test for each comparison.

1) « ...[A]mong parasites of fish, acanthocephalans and nemato des show little host specificity, whereas monogeneans seem to be highly specific. » (e.g., Sasal *et al.*, 1999 ; pg. 437).

Mean index values for the parasites of fish in Appendix I support this statement. The 19 species of acanthocephalans had a mean index value of 4.28 ± 0.95, and the 26 species of nematodes of fishes had a mean index value of 2.71 ± 0.73. By comparison, the 130 species of monogeneans had a mean index value of 0.41 ± 0.13. Wilcoxon signed-rank tests suggest that monogeneans exhibit significantly greater host specificity (at $p = 0.05$ level) than both acanthocephalans and nematodes ($p = 7.71e\text{-}07$, $p = 0.0034$, respectively).

2) « In both marine and freshwater fish, monogeneans as a group are possibly the most host-specific of all fish parasites. » (Poulin, 1992 ; pg. 753).

The mean specificity index values for the groups of fish parasites included in Appendix I support this statement with only one exception. The mean index value for the 109 species of digeneans was 2.60 ± 0.33. The mean index value for the 108 copepod species was 2.93 ± 0.37. As noted above, the mean index values for acanthocephalans was 4.28± 0.95, that for nematodes was 2.71 ± 0.73, and that for monogeneans was 0.41 ± 0.13. Individual Wilcoxon signed-rank tests comparing monogeneans to digeneans, copepods, acanthocephalans and nematodes were all significant at the

$p = 0.05$ level ($p = 4.595e-09$, $p = 1.494e-07$, $7.7111e-07$, $p = 0.000343$, respectively). The 44 species of fish cestodes however, had a mean index value lower than that of the monogeneans (0.01 ± 0.01 versus 0.41 ± 0.13). The results of the Wilcoxon signed-rank test comparing the index values of monogeneans and cestodes suggest the cestodes are significantly more host specific ($p = 0.02$) than the monogeneans. It is important to note, however, that, whereas the majority of the other fish parasite groups in Appendix I parasitize teleosts, the cestode groups included parasitize elasmobranchs. It would be very interesting to investigate this question using cestodes of teleosts because they are generally perceived to be less host specific than the cestodes of elasmobranchs. In which case, elasmobranchs should not be included as 'fishes' in these kinds of comparisons.

3) Ectoparasites [of fishes] are more host-specific than endoparasites. (Rohde & Heap, 1998).

The mean index values for the species in Appendix I that fall into these two groups support this statement. The mean index value for all ectoparasites of fishes (copepods and monogeneans) was : 1.56 ± 0.20 ($n = 238$). The mean index value for all endoparasites of fishes (i.e., acanthocephalans, nematodes, and digeneans) was 2.83 ± 0.29 ($n = 154$). The Wilcoxon signed-rank test was significant ($p = 3.507e-05$). Cestodes were not included in this comparison for the reasons described in comparison 2, above.

4) « ...[P]arasitic worms with direct life cycles...are more host specific than the worms that have an indirect cycle. » (Noble *et al.*, 1989 ; pg. 501).

This statement also appears to be supported by the data in Appendix I. The mean index value for the species of worms presumed to possess direct life-cycles, which from the data in Appendix I include the monogeneans and the entomogenous nematodes only, is 0.90 ± 0.17 ($n = 151$). Whereas the mean index value for the species of worms presumed to possess indirect life cycles (acanthocephalans, digeneans, cystidicolid nematodes and cestodes) is 2.22 ± 0.24 ($n = 201$). The difference between these two groups was significant using the Wilcoxon signed-rank test ($p = 0.00158$).

5) Monogeneans exhibit a high degree of host specificity at the species level, but rather low specificity at the generic level. (see Llewellyn, 1957)

Comparison of the mean generic specificity index value for each of the 21 non-monotypic genera of monogeneans with the generic index value based on the full spectrum of hosts of all species in each genus allows Llewellyn's observation to be addressed. In 16 of the 21 genera the mean generic index values were at least 5 index points lower than the index value calculated for the genus as a whole ; the generic values for six genera are greater than 7 index points above the mean generic index values. As is apparent from Table II, these differences are more marked in the monogeneans than in any of the other parasite groups, providing support for

Llewellyn's observation. If it were not for the fact that so many of the monogenean species exhibit oioxenous specificity, and thus have index values of 0, this question could be more directly addressed by comparing the mean generic index value to the generic index value.

6) The degree of host specificity exhibited by 'ticks' has been controversial (e.g., Hoogstraal & Aeschlimann, 1982 ; Klompen *et al.*, 1996 ; Cumming, 1998).

The tick data analyzed here (which, admittedly, are very limited) result in a mean species host specificity index value of 5.81 ± 0.81 (n = 19). Although we were not able to include the tick data of Cumming (1998) in Appendix I, because of the lack of data on host species identities, the data provided indicate that a number of these species are less host specific than all of the 700 taxa included in Appendix I. At a minimum (i.e., when only data on order and class of host are included) the host specificity index values for the 14 species of ticks that parasitize hosts in 3 classes treated by Cumming (1998) exceed a specificity index value of 9.6. By comparison, the mean index values for the other groups of arthropods parasitizing vertebrates from Appendix I were : lice 0.88 ± 0.50 (n = 8), harpyrhynchid mites 0.62 ± 0.18 (n=114), and fleas 6.49 ± 0.37 (n = 53). The results of Wilcoxon signed-rank tests suggest ticks are significantly less host specific than lice and mites, but not fleas (p = 0.00980, p = 1.754e-13, and p = 0.0954). These values are certainly consistent with the notion expressed previously by many authors (e.g., Marshall, 1981 ; Fain, 1994) that arthropods that are intimately associated with their hosts for extended periods of their lives tend to be much more host specific than those that are less intimately associated with their hosts for only brief periods of time.

Testing the above generalizations was not our main intention. Rather it was our intention to develop a mechanism that would facilitate the consistent comparisons of host specificity at different taxonomic levels and among disparate taxa. There currently exists disagreement about terms used to refer to host specificity. In some cases, even when terms are used routinely, their definitions are vague and there is disagreement about how they should be applied. We favor a quantitative index of specificity that increases the precision of the terms used to describe host specificity in parasitology, and perhaps also ecology, in general. The index described above allows quantitative comparisons of specificity patterns among distantly related groups of hosts and parasites. However the power of the index developed here depends on detailed and accurate host specificity data. If broader questions are to be addressed, generation of this type of data is strongly encouraged for as many parasite species as possible and with as broad geographic sampling as possible. It is our hope that this index will allow parasite systematists and ecologists to assess hypotheses about specificity in a more precise and reproducible way, and perhaps even to reveal patterns that would not otherwise have been detected.

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Appendix I. Host specificity of selected parasite species.

PARASITES			HOSTS						
Families	Species	Source	No. species	No. genera	No. families	No. orders	No. classes	Rank	Species Index (HS_s)
ALLOCREADIIDAE	*Bunodera eucliae*	Caira, 1989; Gibson, 1996	4	4	2	2	1	45665798	7.65959105
n (genera) = 5	*Bunodera luciopercae*	Caira, 1989; Gibson, 1996	35	25	12	10	1	398293445	8.60020316
n (species) = 18	*Bunodera mediovitellata*	Caira, 1989; Gibson, 1996	2	2	1	1	1	1001	3.00043408
	Bunodera saccaluta	Caira, 1989; Gibson, 1996	7	6	4	3	1	91327596	7.96060203
	Bunoderella metteri	Caira, 1989; Gibson, 1996	2	2	2	1	1	398293445	8.60020316
	Crepidostomum auriculatum	Caira, 1989; Gibson, 1996	6	2	1	1	1	1005	3.00216606
	Crepidostomum auritum	Caira, 1989; Gibson, 1996	1	1	1	1	1	1	0.00000000
	Crepidostomum brevivitellum	Caira, 1989; Gibson, 1996	2	2	2	2	1	45663801	7.65957206
	Crepidostomum cooperi	Caira, 1989; Gibson, 1996	38	21	12	11	1	440245718	8.64369514
	Crepidostomum cornutum	Caira, 1989; Gibson, 1996	26	17	9	7	1	269119489	8.42994515
	Crepidostomum farionis	Caira, 1989; Gibson, 1996	47	18	10	9	1	355234538	8.55051518
	Crepidostomum fausti	Caira, 1989; Gibson, 1996	1	1	1	1	1	1	0.00000000
	Crepidostomum hiodontos	Caira, 1989; Gibson, 1996	1	1	1	1	1	1	0.00000000
	Crepidostomum ictaluri	Caira, 1989; Gibson, 1996	7	3	1	1	1	2004	3.30189772
	Crepidostomum illinoiense	Caira, 1989; Gibson, 1996	3	2	2	2	1	45663802	7.65957207
	Crepidostomum isostomum	Caira, 1989; Gibson, 1996	8	6	4	3	1	91327597	7.96060203
	Crepidostomum serpentinum	Caira, 1989; Gibson, 1996	1	1	1	1	1	1	0.00000000
	Paracreptotrematina limi	Caira, 1989; Gibson, 1996	1	1	1	1	1	1	0.00000000
HEMIURIDAE	*Aphanurus stossichi*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
n (genera) = 18	*Aponurus argentini*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
n (species) = 50	*Aponurus califonicus*	Love & Moser, 1983	2	2	2	2	1	45663801	7.65957206
	Aponurus laguncuius	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Aponurus pacificus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Brachyphallus amuruensis	Love & Moser, 1983	3	2	2	2	1	45663801	7.65957206
	Brachyphallus crenatus	Love & Moser, 1983	18	14	10	8	1	312540827	8.49490676
	Brachyphallus parvus	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
	Bunocotyle mugilis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Derogenes crassus	Love & Moser, 1983	2	2	2	2	1	45663801	7.65957206
	Derogenes infirmus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Derogenes marcostoma	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Derogenes varicus	Love & Moser, 1983	49	28	16	10	2	2803855721	9.44775566
	Deropegus spina	Love & Moser, 1983	4	2	1	1	1	2998	3.47683163
	Dichadena galeata	Love & Moser, 1983	1	1	1	1	1	1	0.00000000

DIGENEA		*Dinosma oregoneensis*	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
		Dinosma pectoralis	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
		Dinosma tortum	Love & Moser, 1983	3	2	2	1	1	375252	5.57432302
		Dinurus barbatus	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
		Dinurus breviductus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Dinurus euthynni	Love & Moser, 1983	3	3	1	1	1	2000	3.30103000
		Dinurus longisinus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Dinurus scombri	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
		Dinurus tornatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Dissosaccus laevis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Ectenurus americanus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Ectenurus lepidocybii	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Ectenurus lepidus	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
		Ectenurus virgulus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Ectenurus yamagutii	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Elytorphallus mexicanus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Genarchopsis muellieri	Love & Moser, 1983	13	10	5	4	2	2540355877	9.40489456
		Genolinea aburame	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Genolinea anura	Love & Moser, 1983	7	6	5	3	1	91698852	7.96236390
		Genolinea laticauda	Love & Moser, 1983	19	17	8	5	1	181527384	8.25894215
		Genolinea lintoni	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Genolinea manteri	Love & Moser, 1983	4	4	3	2	1	46039049	7.66312634
		Genolinea montereyensis	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
		Genolinea tanyopa	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
		Glomericirrus ulmeri	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
		Gonocerca haedrichi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Gonocerca oregonensis	Love & Moser, 1983	3	3	2	2	1	45664800	7.65958156
		Gonocerca oshoro	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Gonocerca phycidis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Gonocerella pacifica	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Gonocerella trachinoti	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Hemiurus communis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Hemiurus levinseni	Love & Moser, 1983	20	15	8	6	2	2629434956	9.41986243
		Hemiurus luehei	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Hemiurus odhneri	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	LEPOCREADIIDAE	*Bianium plicitum*	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
	n (genera) = 11	*Cephalolepidapedon saba*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	n (species) = 41	*Dihemistophenus fragilis*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Dihemistophenus lydiae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Echeneidocoelium indicum	Love & Moser, 1983	2	2	1	1	1	2	0.30103000
		Labifer balli	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Labifer secundus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepidapedon antimorae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepidapedon calli	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
		Lepidapedon cascadensis	Love & Moser, 1983	2	1	1	1	1	2	0.30103000

	Lepidapedon elongatum	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
	Lepidapedon epinepheli	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepidapedon filiformis	Love & Moser, 1983	7	6	5	3	1	91698852	7.96236390
	Lepidapedon hancocki	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
	Lepidapedon luteum	Love & Moser, 1983	3	1	1	1	1	3	0.47712125
	Lepidapedon microlyleum	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepidapedon nicolli	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepidapedon oregonensis	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
	Lepidapedon yaquina	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
	Lepocreadium areolatum	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium bimarinum	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium bravoae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium californianum	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium ghanensis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium manteri	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium scombri	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Lepocreadium setiferoides	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Neolabrifer bravoae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Neolepidapedon medialunae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Neolepidapedon pugetense	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
	Neolepidapedon retursum	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Neolepidapedon sebastisci	Love & Moser, 1983	9	1	1	1	1	9	0.95424251
	Opechona alaskensis	Love & Moser, 1983	10	3	3	3	1	90952358	7.95881396
	Opechona bacillaris	Love & Moser, 1983	3	3	3	3	1	90952351	7.95881393
	Opechona occidentalis	Love & Moser, 1983	10	2	2	2	1	45663809	7.65957213
	Opechona olssoni	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Opechona orientalis	Love & Moser, 1983	3	3	3	2	1	46038051	7.66311693
	Opechona parvasoma	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Opechona pharyngodactyla	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Opechona theragrae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Pseudocreadium diodontis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
GYRODACTYLIDAE	*Gyrodactylus abalonia*	Beverley-Burton, 1984	9	8	5	5	1	180410686	8.25626226
n (genera) = 1	*Gyrodactylus adspersi*	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
n (species) = 35	*Gyrodactylus aldrichi*	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus alexanderi	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus aquilinus	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus atratuli	Beverley-Burton, 1984	3	2	2	1	1	375252	5.57432302
	Gyrodactylus bairdi	Beverley-Burton, 1984	2	1	1	1	1	2	0.30103000
	Gyrodactylus bullatarudis	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus cameroni	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus canadensis	Beverley-Burton, 1984	3	3	1	1	1	2000	3.30103000
	Gyrodactylus colemanensis	Beverley-Burton, 1984	2	2	1	1	1	1001	3.00043408
	Gyrodactylus commersoni	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus couesius	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
	Gyrodactylus dechtiari	Beverley-Burton, 1984	2	1	1	1	1	2	0.30103000

PLATYHELMINTHES		*Gyrodactylus etheostomae*	Beverley-Burton, 1984	2	1	1	1	1	2	0.30103000
		Gyrodactylus eucaliae	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus freemani	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus funduli	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Gyrodactylus goerani	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus groenlandicus	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus harengi	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus hoffmani	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus lacusgrandis	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus limi	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus macrochiri	Beverley-Burton, 1984	3	2	1	1	1	1002	3.00086772
		Gyrodactylus nainum	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus nebulosus	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus nerkae	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus pleuronecti	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus plumbeae	Beverley-Burton, 1984	1	1	1	1	1	1	0.00000000
		Gyrodactylus prolongus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Gyrodactylus salmonis	Beverley-Burton, 1984	5	3	1	1	1	2002	3.30146407
		Gyrodactylus spathuatus	Beverley-Burton, 1984	3	2	1	1	1	1002	3.00086772
		Gyrodactylus stephanus	Hargis, 1957	3	2	2	2	1	45663802	7.65957207
		Gyrodactylus stunkardi	Beverley-Burton, 1984	4	3	3	2	1	46038052	7.66311694
	DACTYLOGYRIDAE	*Amphibdelloides narcine*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (genera) = 8	*Ancyrocephalus balisticus*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (species) = 12	*Ancyrocephalus felis*	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Ancyrocephalus lactophrys	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Ancyrocephalus parvis	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Hamatopeduncularia bagre	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Pseudohalitrema carbunculus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Pseudohalitrema mugilidus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Tetrancystrum longiphallus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Diplectatum bilobatus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Rhamnocercus bairdiella	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Rhabdosynochus rhabosynochus	Hargis, 1957	1	1	1	1	1	1	0.00000000
	MONOCOTYLIDAE	*Calicotyle kroyeri*	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
	n (genera) = 16	*Calicotyle palombi*	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
	n (species) = 40	*Calicotyle stossichi*	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Calicotyle urolophi	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Clemacotyle australis	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Decacotyle floridana	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Decacotyle lymmae	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Decacotyle tetrakordyle	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Dendromonocotyle ardae	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Dendromonocotyle octodiscus	Hargis, 1957; Chisholm et al., 2001	3	2	2	1	1	375252	5.57432302
		Dictyocotyle coeliaca	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000

MONOGENEA		*Dionchus rachycentris*	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Dionchus ramorae	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Empruthotrema dasyatidis	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Empruthotrema raiae	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Empurthotrema quindecima	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Heterocotyle aetobatus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Heterocotyle americana	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Heterocotyle capricornensis	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Heterocotyle pseudominima	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Loimopapillosum dasyatis	Hargis, 1957	2	1	1	1	1	1	0.00000000
		Loimos sciiodon	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Loimosina wilsoni	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Merizocotyle australensis	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Merizocotyle icopae	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Merizocotyle urolophi	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Monocotyle corali	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Monocotyle deademalis	Hargis, 1957	2	1	1	1	1	2	0.30103000
		Monocotyle helicophallus	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Monocotyle multiparous	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Monocotyle pricei	Hargis, 1957	2	1	1	1	1	2	0.30103000
		Monocotyle spiremae	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
		Neoheterocotyle inpristi	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Neoheterocotyle rhinobatidis	Chisholm, et al 2001	1	1	1	1	1	1	0.00000000
		Neoheterocotyle rhinobatis	Chisholm, et al 2001	1	1	1	1	1	1	0.00000000
		Neoheterocotyle rhynchobatus	Chisholm, et al 2001	1	1	1	1	1	1	0.00000000
		Thaumatocotyle longicirrus	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Thaumatocotyle pseudodasybatis	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Thaumatocotyle retorta	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Troglocephalus rhinobatidis	Chisholm et al., 2001	1	1	1	1	1	1	0.00000000
	CAPSALIDAE	*Benedenia posterocolpa*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (genera) = 2; n (species) = 2	*Entobdella corona*	Hargis, 1957	3	1	1	1	1	3	0.47712125
	HEXABOTHRIIDAE	*Dasyonchocotyle spiniphalus*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (genera) = 3	*Heteronchocotyle leucas*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (species) = 4	*Squalonchocotyle inpristi*	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Squalonchocotyle tiburonis	Hargis, 1957	1	1	1	1	1	1	0.00000000
	MAZOCRAEIDAE	*Clupaeocotyle brevoortia*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (genera) = 3	*Clupaeocotyle megaconfibula*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (species) = 5	*Cunea brevoortea*	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Mesocraeoides georgei	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Mesocraeoides opisthonema	Hargis, 1957	1	1	1	1	1	1	0.00000000
	DISCOCOTYLIDAE	*Bicotylophora trachinoti*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (genera) = 2	*Tagia bairdiella*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	n (species) = 4	*Taiga cupida*	Hargis, 1957	1	1	1	1	1	1	0.00000000
		Taiga micropogone	Hargis, 1957	1	1	1	1	1	1	0.00000000

DICLYDOPHORIDAE	*Choricotyle aspinocorda*	Hargis, 1957	1	1	1	1	1	1	0.00000000
n (genera) = 2	*Choricotyle lusianensis*	Hargis, 1957	1	1	1	1	1	1	0.00000000
n (species) = 5	*Choricotyle prionoti*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Choricotyle sinosynoscioni	Hargis, 1957	2	1	1	1	1	2	0.30103000
	Petocotyle minima	Hargis, 1957	1	1	1	1	1	1	0.00000000
MICROCOTYLIDAE	*Axinoides gracilis*	Hargis, 1957	1	1	1	1	1	1	0.00000000
n (genera) = 6	*Axinoides raphidoma*	Hargis, 1957	1	1	1	1	1	1	0.00000000
n (species) = 15	*Axinoides truncatus*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Cemocotyle carangus	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Heteraxine carangus	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Heteraxine xanthophyllus	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Metamicrocotyla macracantha	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle archosargi	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle heteracantha	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle pogoniae	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle pomacanthae	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle pomatome	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle pseudoheteracantha	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Microcotyle pseudomugilus	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Pyragraphorus hippos	Hargis, 1957	1	1	1	1	1	1	0.00000000
GASTROCOTYLIDAE	*Amphipolycotyle cloroscombrus*	Hargis, 1957	1	1	1	1	1	1	0.00000000
n (genera) = 8	*Lithidocotyle acanthophallus*	Hargis, 1957	2	1	1	1	1	2	0.30103000
n (species) = 8	*Protomicrocotyle mirabilis*	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Pseudaxine mexicana	Hargis, 1957	2	1	1	1	1	2	0.30103000
	Pseudomazocraes selene	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Scomberocotyle scomberomore	Hargis, 1957	2	1	1	1	1	2	0.30103000
	Thoracocotyle croceà	Hargis, 1957	1	1	1	1	1	1	0.00000000
	Vallezia oligoplitis	Hargis, 1957	1	1	1	1	1	1	0.00000000
ONCHOBOTHRIIDAE	*Acanthobothrium bajaense*	Appy & Dailey, 1973	1	1	1	1	1	1	0.00000000
n (genera) = 8	*Acanthobothrium bullardi*	Ghoshroy & Caira, 2001	1	1	1	1	1	1	0.00000000
n (species) = 36	*Acanthobothrium dasi*	Ghoshroy & Caira, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium dollyae	Caira & Burge, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium heterodonti	Caira & Zahner, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium maryanskii	Caira & Burge, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium puertecitense	Caira & Zahner, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium rajivi	Ghoshroy & Caira, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium royi	Caira & Burge, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium santarosaliense	Caira & Zahner, 2001	1	1	1	1	1	1	0.00000000
	Acanthobothrium sobaroni	Ghoshroy & Caira, 2001	1	1	1	1	1	1	0.00000000
	Biloculuncus pritchardae	Caira & Ruhnke, 1990	1	1	1	1	1	1	0.00000000
	Calliobothirum eschrichtii	Nasin, Caira & Euzet, 1997	1	1	1	1	1	1	0.00000000
	Calliobothrium evani	Nasin, Caira & Euzet, 1997	1	1	1	1	1	1	0.00000000
	Calliobothrium hayhowi	Nasin, Caira & Euzet, 1997	1	1	1	1	1	1	0.00000000
	Calliobothrium pellucidum	Nasin, Caira & Euzet, 1997	1	1	1	1	1	1	0.00000000
	Calliobothrium riseri	Nasin, Caira & Euzet, 1997	1	1	1	1	1	1	0.00000000

CESTODA		*Calliobothrium violae*	Nasin, Caira & Euzet, 1997	1	1	1	1	1	1	0.00000000
		Erudituncus musteli	Healy, Scholz & Caira, 2001	1	1	1	1	1	1	0.00000000
		Pachybothrium hudsoni	Caira & Pritchard, 1986	1	1	1	1	1	1	0.00000000
		Pedibothirum kerkhami	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothirum longispine	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothrium brevispine	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothrium globicephalum	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothrium maccallumi	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothrium manteri	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothrium servattorum	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pedibothrium toliarense	Caira & Rasolofonirina, 1998	1	1	1	1	1	1	0.00000000
		Pedibothrium veravalensis	Caira, 1992	1	1	1	1	1	1	0.00000000
		Pinguicollum pinguicollum	Caira & Keeling, 1996	4	1	1	1	1	4	0.60205999
		Platybothrium harpago	Healy, 2002	1	1	1	1	1	1	0.00000000
		Platybothrium hypoprioni	Healy, 2002	1	1	1	1	1	1	0.00000000
		Platybothrium auriculatum	Healy, 2002	1	1	1	1	1	1	0.00000000
		Platybothrium cervinum	Healy, 2002	1	1	1	1	1	1	0.00000000
		Platybothrium parvum	Healy, 2002	1	1	1	1	1	1	0.00000000
		Platybothrium spinulifera	Healy, 2002	1	1	1	1	1	1	0.00000000
	LITOBOTHRIIDAE	*Litobothrium alopias*	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
	n (genera) = 1	*Litobothrium amplifica*	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
	n (species) = 8	*Litobothrium amsichensis*	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
		Litobothrium coniformis	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
		Litobothrium daileyi	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
		Litobothrium gracile	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
		Litobothrium janovyi	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
		Litobothrium nickoli	Olson & Caira, 2001	1	1	1	1	1	1	0.00000000
	PSEUDOPHYLLIDEA	*Cephalochlamys compactus*	Jackson & Tinsley, 2001	5	2	2	1	1	375254	5.57432533
	n (genera) = 2	*Cephalochlamys namaquensis*	Jackson & Tinsley, 2001	2	2	2	1	1	375251	5.57432186
	n (species) = 3	*Paracephalochlamys papilionis*	Jackson & Tinsley, 2001	1	1	1	1	1	1	0.00000000
ACANTHOCEPHALA	NEOECHINORHYNCHIDAE	*Floridosentus elongatus*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	n (genera) = 6	*Gracilisentis gracilisentis*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	n (species) = 19	*Microsentis wardae*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Neoechinorhynchus agilis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Neoechinorhynchus carpiodi	Arai, 1989; Margolis & Arthur, 1979	1	1	1	1	1	1	0.00000000
		Neoechinorhynchus chilkaense	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Neoechinorhynchus crassus	Arai, 1989; Margolis & Arthur, 1979	7	5	3	3	1	90954348	7.95882346
		Neoechinorhynchus criststus	Arai, 1989; Margolis & Arthur, 1979	9	6	4	3	1	91327598	7.96060204
		Neoechinorhynchus cylindratus	Arai, 1989; Margolis & Arthur, 1979	16	13	7	5	1	181155168	8.25805073
		Neoechinorhynchus notemigoni	Arai, 1989; Margolis & Arthur, 1979	1	1	1	1	1	1	0.00000000
		Neoechinorhynchus pungitius	Arai, 1989; Margolis & Arthur, 1979	5	5	4	4	1	135867648	8.13311606
		Neoechinorhynchus rutili	Arai, 1989	40	26	14	10	1	399020069	8.60099474
		Neoechinorhynchus saginatus	Arai, 1989	12	8	4	3	1	91329588	7.96061150
		Neoechinorhynchus salmonis	Arai, 1989	14	10	5	4	1	136243878	8.13431700
		Neoechinorhynchus strigosus	Arai, 1989; Margolis & Arthur, 1979	6	5	5	4	1	136238905	8.13430114
		Neoechinorhynchus tenellus	Arai, 1989; Margolis & Arthur, 1979	5	3	3	2	1	46038053	7.66311695

		Neoechinorhynchus tumidus	Arai, 1989; Margolis & Arthur, 1979	11	8	4	4	1	135870636	8.13312561
		Octospinifer macilentus	Arai, 1989; Margolis & Arthur, 1979	3	1	1	1	1	3	0.47712125
		Tanaorhamphus longirostris	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
NEMATODA	CYSTIDICOLIDAE	*Ascarophis curvicauda*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	n (genera) = 9	*Ascarophis filiformis*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	n (species) = 26	*Ascarophis morrhuae*	Margolis & Arthur, 1979; Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Ascarophis pacificus	Love & Moser, 1983	6	6	5	5	1	180408696	8.25625747
		Ascarophis sebastodis	Margolis & Arthur, 1979; Love & Moser, 1983	21	10	8	4	1	137351681	8.13783398
		Ascarophis skrjabini	Love & Moser, 1983	4	3	2	2	1	45664801	7.65958157
		Caballeronema wardlei	Margolis & Arthur, 1979; Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Ctenascarophis gastricus	Love & Moser, 1983	2	2	1	1	1	1001	3.00043408
		Cystidicola cristivomeri	Margolis & Arthur, 1979	1	1	1	1	1	1	0.00000000
		Cystidicola farionis	Margolis & Arthur, 1979	23	12	6	5	1	180784922	8.25716221
		Cystidicola stigmatura	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Cystidicola tenuissima	Love & Moser, 1983	6	4	2	2	1	45665800	7.65959107
		Cystidicoloides prevosti	Margolis & Arthur, 1979	1	1	1	1	1	1	0.00000000
		Cystidicoloides tenuissima	Margolis & Arthur, 1979	15	8	4	4	1	135870640	8.13312562
		Metabronema laticauda	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Parascarophis galeata	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Salvelinema ishii	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Salvelinema salmincola	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
		Salvelinema walkeri	Love & Moser, 1983	4	2	1	1	1	1003	3.00130093
		Spinitectus beaveri	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Spinitectus carolini	Margolis & Arthur, 1979	6	5	3	2	1	46040047	7.66313576
		Spinitectus echenei	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Spinitectus gordani	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Spinitectus gracilis	Margolis & Arthur, 1979	18	16	9	6	1	225691217	8.35351466
		Spinitectus mollis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Spinitectus pacificus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	ALLANTONEMATIDAE	*Heterotylenchus autumnalis*	Poinar, 1979	4	3	1	1	1	2001	3.30124709
	DIPLOGASTERIDAE	*Mesodiplogaster lheritieri*	Poinar, 1979	4	4	3	1	1	750499	5.87535012
	HETERORHABDITIDAE	*Heterorhabditis bacteriophora*	Poinar, 1979	1	1	1	1	1	1	0.00000000
	n (genera) = 1; n (species) = 2	*Heterorhabditis heliothidis*	Poinar, 1979	1	1	1	1	1	1	0.00000000
	MERMITHIDAE	*Agamermis decaudata*	Poinar, 1979	10	6	3	2	1	46041046	7.66314518
	n (genera) = 10	*Filipjevimermis leipsandra*	Poinar, 1979	2	2	1	1	1	1001	3.00043408
	n (species) = 12	*Gastromermis viridis*	Poinar, 1979	4	2	1	1	1	1003	3.00130093
		Hydromermis churchillensis	Poinar, 1979	5	3	2	1	1	376252	5.57547882
		Hydromermis contorta	Poinar, 1979	6	4	1	1	1	3000	3.47712125
		Isomermis lairdi	Poinar, 1979	6	1	1	1	1	6	0.77815125
		Isomermis wisconsiensis	Poinar, 1979	3	2	1	1	1	2002	3.30146407
		Limnomerimis rosea	Poinar, 1979	2	1	1	1	1	2	0.30103000
		Mermis nigrescens	Poinar, 1979	58	37	12	5	1	183010057	8.26247496
		Mesomermis flumenalis	Poinar, 1979	9	2	1	1	1	1008	3.00346053

	Octomyomermis muspratti	Poinar, 1979	10	2	1	1	1	1009	3.00389117
	Strelkovimermis peterseni	Poinar, 1979	3	1	1	1	1	3	0.47712125
NEOTYLENCHIDAE	*Deladenus siricidicola*	Poinar, 1979	6	3	2	2	1	45664803	7.65958159
STEINERNEMATIDAE	*Neoaplectana bibionis*	Poinar, 1979	3	2	1	1	1	1002	3.00086772
n (genera) = 1	*Neoaplectana carpocapsae*	Poinar, 1979	7	6	6	3	1	92069112	7.96411395
n (species) = 4	*Neoaplectana glaseri*	Poinar, 1979	5	5	4	2	1	46412299	7.66663308
	Neoaplectana leucaniae	Poinar, 1979	2	2	2	1	1	375251	5.57432186
CALIGIDAE	*Anuretes heckelii*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
n (genera) = 10	*Anuretes quadrilaterus*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
n (species) = 80	*Caligodes laciniatus*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus asymmetricus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus auxisi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus belones	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus bonito	Love & Moser, 1983	8	7	5	2	1	46785547	7.67011171
	Caligus chelifer	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus chorinemi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus clemensi	Margolis & Arthur, 1979; Love & Moser, 1983	13	8	7	6	2	2629059755	9.41980046
	Caligus confusus	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
	Caligus constrictus	Love & Moser, 1983	2	2	2	1	1	375251	5.57432186
	Caligus coryphaenae	Love & Moser, 1983	12	8	7	3	2	2496552369	9.39734068
	Caligus curtus	Margolis & Arthur, 1979	7	7	4	3	2	2495440590	9.39714723
	Caligus diaphanus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus elongatus	Love & Moser, 1984	23	23	17	12	2	2887757255	9.46056068
	Caligus epidemicus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus germoi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus glandifer	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus hobsoni	Love & Moser, 1983	15	12	7	3	1	92444334	7.96588030
	Caligus irritans	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus klawei	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus lacustris	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus lunatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus macarovi	Margolis & Arthur, 1979; Love & Moser, 1983	2	2	2	2	1	45663801	7.65957206
	Caligus minimus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus mutabilis	Love & Moser, 1983	9	7	5	1	1	1496998	6.17522122
	Caligus olsoni	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus orientalis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus patulus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus pectinatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus pelamydis	Love & Moser, 1983	3	3	2	1	1	376250	5.57547651
	Caligus platytarsis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus praetextus	Love & Moser, 1983	4	4	4	2	2	2450523302	9.38925884
	Caligus productus	Love & Moser, 1983	17	12	8	2	1	47898307	7.68032016
	Caligus quadatus	Love & Moser, 1983	5	5	4	1	1	1123749	6.05066932
	Caligus rectus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	Caligus robustus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000

COPEPODA		*Caligus rufimaculatus*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Caligus serratus	Love & Moser, 1983	3	3	2	2	1	45664800	7.65958156
		Caligus spinosurculus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Caligus tenax	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Caligus tenicaudatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Caligus tenuifrucatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Dentigryps curtus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus abdominis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus appendiculatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus bifidus	Love & Moser, 1983	4	4	2	1	1	377248	5.57662695
		Lepeophtheirus bifurcatus	Love & Moser, 1983	3	3	2	2	1	45664800	7.65958156
		Lepeophtheirus brachyurus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus breviventris	Margolis & Arthur, 1979; Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus constrictus	Love & Moser, 1983	3	1	1	1	1	3	0.47712125
		Lepeophtheirus crassus	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
		Lepeophtheirus cuneifer	Love & Moser, 1983	10	10	7	6	2	2629061735	9.41980078
		Lepeophtheirus dissimulatus	Love & Moser, 1983	8	8	7	4	1	136981414	8.13666164
		Lepeophtheirus edwardsi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus emiens	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus goniistii	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus hastatus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus hexagrammi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus hospitalis	Margolis & Arthur, 1979; Love & Moser, 1983	6	6	3	3	1	90955342	7.95882821
		Lepeophtheirus longipes	Love & Moser, 1983	5	4	4	2	1	46411303	7.66662376
		Lepeophtheirus longispinosus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus nanaimoensis	Margolis & Arthur, 1979	1	1	1	1	1	1	0.00000000
		Lepeophtheirus nordmanni	Margolis & Arthur, 1979; Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus oblitus	Margolis & Arthur, 1979; Love & Moser, 1983	7	2	2	1	1	375256	5.57432764
		Lepeophtheirus parvicruris	Margolis & Arthur, 1979; Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus parviventris	Margolis & Arthur, 1979; Love & Moser, 1983	21	18	11	5	2	2586739228	9.41275265
		Lepeophtheirus parvus	Love & Moser, 1983	3	3	2	1	1	376250	5.57547651
		Lepeophtheirus paulus	Margolis & Arthur, 1979; Love & Moser, 1983	6	1	1	1	1	6	0.77815125
		Lepeophtheirus pollachius	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Lepeophtheirus pravipes	Margolis & Arthur, 1979; Love & Moser, 1983	4	4	4	3	2	2495437602	9.39714671
		Lepeophtheirus salmonis	Love & Moser, 1983	14	7	5	4	1	136240902	8.13430751
		Lepeophtheirus thompsoni	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Pseudocaligus apodus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Pseudolepeophtheirus longicauda	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Pupulina brevicauda	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Pupulina minor	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Sciaenophilus bennetti	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
		Tuxophorus caligodes	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	PANDARIDAE	*Demoleus heptapus*	Love & Moser, 1983	2	2	2	2	1	45663801	7.65957206
	n (genera) = 12	*Demoleus latus*	Love & Moser, 1983	1	1	1	1	1	1	0.00000000

ARTHROPODA		n (species) = 28	*Dinemoura discrepans*	Love & Moser, 1983	2	1	1	1	1	2	0.30103000
			Dinemoura latifolia	Love & Moser, 1983	5	5	4	2	1	46412299	7.66663308
			Dinemoura producta	Love & Moser, 1983	6	6	4	2	1	46413295	7.66664240
			Echthrogaleus coleoptratus	Love & Moser, 1983	6	6	5	4	2	2540351000	9.40489373
			Echthrogaleus denticulatus	Love & Moser, 1983	4	4	4	2	1	46411302	7.66662375
			Gangliopus pyriformis	Love & Moser, 1983	3	3	3	2	1	46038051	7.66311693
			Nesippus borealis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Nesippus crypturus	Love & Moser, 1983	5	3	2	1	1	376252	5.57547882
			Nesippus gracilis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Nesippus orientalis	Love & Moser, 1983	6	3	2	1	1	376253	5.57547997
			Nesippus tirgis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Nogagus ambiguus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Pagina tunica	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Pandarus bicolor	Love & Moser, 1983	8	8	6	5	2	2584892945	9.41244256
			Pandarus carcharini	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Pandarus cranchii	Love & Moser, 1983	10	7	4	2	1	46414293	7.66665174
			Pandarus floridanus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Pandarus katoi	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Pandarus satyrus	Love & Moser, 1983	4	4	3	2	1	46039049	7.66312634
			Pandarus sinuatus	Love & Moser, 1983	5	4	3	2	2	2450151050	9.38919286
			Pandarus spinacliacanthiae	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Pannosus japonicus	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
			Perissopus dentatus	Love & Moser, 1983	4	2	2	1	1	375253	5.57432417
			Perissopus oblongatus	Love & Moser, 1983	11	9	8	6	2	2629429016	9.41986145
			Phyllosthyreus cornutus	Love & Moser, 1983	3	3	3	2	1	46038051	7.66311693
			Prosaetes rhinodontis	Love & Moser, 1983	1	1	1	1	1	1	0.00000000
	ACARI	IXODIDAE	*Dermacentor albipictus*	Kennedy & Newman, 1986	8	7	3	2	1	46042038	7.66315454
		n (genera) = 3	*Dermacentor andersoni*	Kennedy & Newman, 1986	25	18	10	4	1	138093141	8.14017211
		n (species) = 19	*Dermacentor variabilis*	Kennedy & Newman, 1986	19	16	9	4	1	137724882	8.13901241
			Haemophyzalis leporis-palustrus	Kennedy & Newman, 1986	9	7	4	3	1	91328592	7.96060676
			Ixodes angustus	Kennedy & Newman, 1986	23	13	6	3	1	90076065	7.95460941
			Ixodes cookei	Kennedy & Newman, 1986	11	10	7	3	1	92442351	7.96587098
			Ixodes echotonae	Kennedy & Newman, 1986	3	3	2	2	1	45664800	7.65958156
			Ixodes hearlei	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
			Ixodes hexagonus	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
			Ixodes kingi	Kennedy & Newman, 1986	5	4	2	2	1	45665799	7.65959106
			Ixodes marmotae	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
			Ixodes marxi	Kennedy & Newman, 1986	5	5	3	3	1	90954346	7.95882346
			Ixodes muris	Kennedy & Newman, 1986	12	10	4	2	1	46417271	7.66667960
			Ixodes pacificus	Kennedy & Newman, 1986	8	8	5	3	1	91700840	7.96237331
			Ixodes rugosis	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
			Ixodes sculptus	Kennedy & Newman, 1986	5	3	3	2	1	46038053	7.66311695
			Ixodes soricis	Kennedy & Newman, 1986	2	1	1	1	1	2	0.30103000
			Ixodes spinipalpus	Kennedy & Newman, 1986	6	6	5	3	1	91698851	7.96236389
			Ixodes texanus	Kennedy & Newman, 1986	8	8	4	2	1	46415284	7.66666101

HARPYRHYNCHIDAE n (genera) = 2 n (species) = 114	*Harpyrhynchus* sp. 1 - 91	Moss, 1979	1	1	1	1	1	1	0.00000000
	Harpyrhynchus brevis	Moss, 1979	29	27	7	1	1	2256213	6.35338010
	Harpyrhynchus coturnix	Moss, 1979	2	2	2	1	1	375251	5.57432186
	Harpyrhynchus cylindripalpis	Moss, 1979	6	6	4	1	1	1124745	6.05105407
	Harpyrhynchus monstrosis	Moss, 1979	9	8	3	2	1	46043032	7.66316391
	Harpyrhynchus n.sp.1	Moss, 1979	2	1	1	1	1	2	0.30103000
	Harpyrhynchus nidulens	Moss, 1979	7	7	5	1	1	1496996	6.17522064
	Harpyrhynchus novoplumeris	Moss, 1979	7	7	5	2	1	46785546	7.67011170
	Harpyrhynchus pilirostris	Moss, 1979	2	2	2	1	1	375251	5.57432186
	Harpyrhynchus plumeris	Moss, 1979	7	5	4	2	1	46412301	7.66663310
	Harpypalpus sp. 1 - 11	Moss, 1979	1	1	1	1	1	1	0.00000000
	Harpypalpus holopus	Moss, 1979	3	3	3	1	1	749501	5.87477222
	Harpypalpus longipes	Moss, 1979	7	6	4	1	1	1124746	6.05105446
	Harpypalpus n.sp. 1	Moss, 1979	2	2	2	1	1	375251	5.57432186
CERATOPHYLLIDAE n (genera) = 16 n (species) = 53	*Amalaraeus athabascae*	Kennedy & Newman, 1986	7	5	2	2	1	45666797	7.65960055
	Amalaraeus dissimilis	Kennedy & Newman, 1986	26	15	6	3	1	92078041	7.96415607
	Amphalius runatus necopinus	Kennedy & Newman, 1986	2	1	1	1	1	2	0.30103000
	Ceratophyllus adustus	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
	Ceratophyllus diphinis	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
	Ceratophyllus gallinae	Kennedy & Newman, 1986	3	3	2	1	1	376250	5.57547651
	Ceratophyllus garei	Kennedy & Newman, 1986	8	7	5	3	1	91699847	7.96236861
	Ceratophyllus lunatus tundrensis	Kennedy & Newman, 1986	10	7	3	2	1	46042040	7.66315456
	Ceratophyllus niger	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
	Ceratophyllus petrochelidoni	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
	Dactylophypsylla comis	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
	Dactylophypsylla rara	Kennedy & Newman, 1986	2	2	2	2	1	45663801	7.65957206
	Dasypsyllus gallinulae perpinnatus	Kennedy & Newman, 1986	3	3	2	1	1	376250	5.57547651
	Foxella ignota	Kennedy & Newman, 1986	11	7	5	2	1	46785550	7.67011174
	Malaraeus bitterrootensis	Kennedy & Newman, 1986	4	3	2	2	1	45664801	7.65958157
	Malaraeus euphorbi	Kennedy & Newman, 1986	5	4	3	2	1	46039050	7.66312635
	Malaraeus telchinus	Kennedy & Newman, 1986	15	9	5	3	1	91701839	7.96237805
	Megabothris abantis	Kennedy & Newman, 1986	31	17	9	4	1	137725878	8.13901555
	Megabothris acerbus	Kennedy & Newman, 1986	5	4	2	1	1	377249	5.57662810
	Megabothris asio	Kennedy & Newman, 1986	35	19	6	3	1	92081984	7.96417467
	Megabothris atrox	Kennedy & Newman, 1986	5	3	2	1	1	376252	5.57547882
	Megabothris calcarifer gregsoni	Kennedy & Newman, 1986	17	8	3	3	1	90957340	7.95883775
	Megabothris clantoni	Kennedy & Newman, 1986	1	1	1	1	1	1	0.00000000
	Megabothris greenlandicus	Kennedy & Newman, 1986	15	8	3	2	1	46043038	7.66316397
	Megabothris lucifer	Kennedy & Newman, 1986	11	7	3	2	1	46042041	7.66315457
	Megabothris quirini	Kennedy & Newman, 1986	40	21	7	4	1	136994264	8.13670238
	Monopsyllus ciliatus protinus	Kennedy & Newman, 1986	20	14	6	3	1	92077049	7.96415139
	Monopsyllus eumolpi	Kennedy & Newman, 1986	18	12	5	3	1	91704812	7.96239212
	Monopsyllus thambus	Kennedy & Newman, 1986	7	5	2	2	1	45666797	7.65960055
SIPHONAPTE	*Monopsyllus tolli*	Kennedy & Newman, 1986	2	2	2	2	1	45663801	7.65957206

R		*Monopsyllus vison*	Kennedy & Newman, 1986	29	16	7	3	1	92448294	7.96589890
A		*Monopsyllus wagneri*	Kennedy & Newman, 1986	25	16	8	4	1	137357610	8.13785273
		Nosopsyllus fasciatus	Kennedy & Newman, 1986	11	8	3	2	1	46043034	7.66316393
		Opisocrostis bruneri	Kennedy & Newman, 1986	10	7	4	3	1	91328593	7.96060677
		Opisocrostis labis	Kennedy & Newman, 1986	5	4	2	2	1	44665799	7.64997511
		Opisocrostis tuberculatus	Kennedy & Newman, 1986	10	6	4	2	1	46413299	7.66664244
		Opisodasys keeni keeni	Kennedy & Newman, 1986	12	7	4	2	1	46414295	7.66665176
		Opisodasys pseudoarctomys	Kennedy & Newman, 1986	8	6	4	2	1	46413297	7.66664242
		Opisodasys vesperalis	Kennedy & Newman,.1986	5	5	4	3	1	91326599	7.96059728
		Orchopeas caedens	Kennedy & Newman, 1986	23	13	5	2	1	46791505	7.67016701
		Orchopeas howardi howardi	Kennedy & Newman, 1986	6	4	1	1	1	3000	3.47712125
		Orchopeas leucopus	Kennedy & Newman, 1986	23	13	4	2	1	46420249	7.66670747
		Orchopeas nepos	Kennedy & Newman, 1986	7	5	2	2	1	45666797	7.65960055
		Orchopeas sextentatus agilis	Kennedy & Newman, 1986	17	14	6	3	1	92077046	7.96415138
		Oropsylla alaskensis	Kennedy & Newman, 1986	6	5	5	2	1	46783556	7.67009323
		Oropsylla arctomys	Kennedy & Newman, 1986	18	13	6	3	1	92076060	7.96414673
		Oropsylla idahoensis	Kennedy & Newman, 1986	18	7	5	3	1	91699857	7.96236866
		Oropsylla rupestris	Kennedy & Newman, 1986	13	9	6	3	1	92070297	7.96411954
		Tarsopsylla coloradensis	Kennedy & Newman, 1986	6	5	3	2	1	46040047	7.66313576
		Thrassis acamantis	Kennedy & Newman, 1986	11	9	3	2	1	46044026	7.66317329
		Thrassis bacchi bacchi	Kennedy & Newman, 1986	5	3	2	2	1	45664802	7.65958158
		Thrassis peteolatus	Kennedy & Newman, 1986	7	4	3	1	1	750502	5.87535185
		Thrassis spenceri	Kennedy & Newman, 1986	5	2	2	2	1	45663804	7.65957209
A	PHILOPTERIDAE	*Cotingocola dimorpha*	Clayton & Price, 1998	1	1	1	1	1	1	0.00000000
L	n (genera) = 1	*Cotingocola fizpatrici*	Clayton & Price, 1998	1	1	1	1	1	1	0.00000000
L	n (species) = 8	*Cotingocola gracilis*	Clayton & Price, 1998	1	1	1	1	1	1	0.00000000
O		*Cotingocola meridae*	Clayton & Price, 1998	2	1	1	1	1	2	0.30103000
P		*Cotingocola parmipaplllae*	Clayton & Price, 1998	2	2	1	1	1	1001	3.00043408
H		*Cotingocola rupicolae*	Clayton & Price, 1998	3	3	1	1	1	2000	3.30103000
A		*Cotingocola stotzi*	Clayton & Price, 1998	1	1	1	1	1	1	0.00000000
G		*Cotingocola teragalis*	Clayton & Price, 1998	3	1	1	1	1	3	0.47712125
		Antrodiella liebmannii	Lindblad, 2000	1	1	1	1	1	1	0.00000000
	n (genera) =25	*Antrodiella semisupina*	Lindblad, 2000	1	1	1	1	1	1	0.00000000
	n (species) = 47	*Antrodiella sp.*	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Aurifaria luteoumbrina	Lindblad, 2000	4	4	4	4	1	135866651	8.13311287
		Ceriporia alachuana	Lindblad, 2000	5	5	4	3	1	91326599	7.96059728
		Ceriporia ferruginicicta	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Ceriporia microspora	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Ceriporia reticulata	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Ceriporia xylostromatoides	Lindblad, 2000	11	10	10	7	1	269478851	8.43052469
		Ceriporiopsis latemarginata	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Ceriporiopsis loweii	Lindblad, 2000	1	1	1	1	1	1	0.00000000

FUNGI	APHYLLOPHORALES	*Ceriporiopsis mucida*	Lindblad, 2000	8	8	7	7	1	268375030	8.42874211
		Ceriporiopsis sp.	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Coriolopsis byrsina	Lindblad, 2000	12	12	10	7	1	269480831	8.43052788
		Coriolopsis polyzona	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Coriolopsis rigida	Lindblad, 2000	13	11	7	6	1	224950728	8.35208740
		Cotylidia aurantiaca	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Cristelloporia dimitia	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Datronia caperata	Lindblad, 2000	10	10	9	7	1	269112564	8.42993397
		Datronia scutellata	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Datronia steroides	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Diplomitoporus costaricensis	Lindblad, 2000	3	3	3	3	1	90952351	7.95881393
		Earliella scabrosa	Lindblad, 2000	7	7	6	4	1	136611155	8.13548616
		Filoboletus gracilis	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Fomes fasciatus	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Fomitopsis feei	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Fuscocerrena portoricensis	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Ganoderma amazonense	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Ganoderma australe	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Gleophyllum striatum	Lindblad, 2000	3	3	2	2	1	45664800	7.65958156
		Gleoporus thelephoroides	Lindblad, 2000	4	4	4	3	1	91325602	7.96059254
		Hexagonia hydnoides	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Hexagonia papyracea	Lindblad, 2000	3	3	3	3	1	90952351	7.95881393
		Hymenochaete berteroi	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Hymenochaete dura	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Hymenochaete epichlora	Lindblad, 2000	2	2	1	1	1	2	0.30103000
		Hymenochaete sp.	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Inonotus dryophilus	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Melanoporella carbonacea	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Microporellus obovatus	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Nigroporus vinosus	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Perenniporia ochroleuca	Lindblad, 2000	3	3	3	2	1	46038051	7.66311693
		Perenniporia roseoisabellina	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Perenniporia tepeitensis	Lindblad, 2000	1	1	1	1	1	1	0.00000000
		Perenniporia tephropora	Lindblad, 2000	5	5	4	4	1	135867648	8.13311606
		Phellinus chryseus	Lindblad, 2000	2	2	2	2	1	45663801	7.65957206
		Phellinus contiguus	Lindblad, 2000	4	4	3	3	1	90953349	7.95881869

Appendix 1. Host specificity of selected parasite species.

APPENDIX II.

Appendix 2. The C++ code for algorithm to compute host specificity rank and corresponding index value.

```
typedef double IndexValue;

IndexValue host_index(const int host_species, const int host_genera,
                      const int host_families, const int host_orders,
                      const int host_classes)
{
 IndexValue value = 0;
 if (host_classes > 1) {
   value = host_index(n_species, n_genera, n_families, n_orders,
                      host_classes-1);
   IndexValue f_index = host_index(host_species, host_genera, host_families,
                      host_orders, 1);
   IndexValue o_index = host_index(host_classes, host_classes, host_classes,
                      host_classes, 1);
   value += f_index - o_index + 1;
 } else if (host_orders > 1) {
   value = host_index(n_species, n_genera, n_families, host_orders-1, 1);
   IndexValue f_index = host_index(host_species, host_genera, host_families,
                      1, 1);
   IndexValue o_index = host_index(host_orders, host_orders, host_orders, 1, 1);
   value += f_index - o_index + 1;
 } else if (host_families > 1) {
   value = host_index(n_species, n_genera, host_families-1, 1, 1);
   IndexValue f_index = host_index(host_species, host_genera, 1, 1, 1);
   IndexValue o_index = host_index(host_families, host_families, 1, 1, 1);
   value += f_index - o_index + 1;
 } else if (host_genera > 1) {
   for (int g = 1; g < host_genera; g++) {
    value += n_species - g + 1;
   }
   value += host_species - host_genera + 1;
   // The approach on the following lines follows the same recursive
   // logic as above, but is less computationally efficient than
   // the code actually used. It produces identical results.
   //
   // value = host_index(n_species, host_genera-1, 1, 1, 1);
   // IndexValue f_index = host_index(host_species, 1, 1, 1, 1);
   // IndexValue o_index = host_index(host_genera, 1, 1, 1, 1);
   // value += f_index - o_index + 1;
 } else {
   value = host_species;
 }
 return value;
}
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References

Arai HP, 1989. Acanthocephala. In : Margolis L, Kabata Z, editors. Guide to the Parasites of Fishes of Canada. Part III. Canadian Special Publication of Fisheries and Aquatic Sciences 107 : 1-84.

Baer JG, 1957. Premier Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés. Institut de Zoologie, Université de Neuchatel. Attinger, Neuchatel, Suisse : 1-324.

Beverley-Burton M, 1984. Monogenea and Turbellaria. In : Margolis L, Kabata Z, editors. Guide to the Parasites of Fishes of Canada. Part I. Canadian Special Publication of Fisheries and Aquatic Sciences 74 : 5-209.

Caira JN, 1989. A revision of the North American papillose Allocreadiidae (Digenea) with independent cladistic analyses of larval and adult forms. Bulletin of the University of Nebraska State Museum 11 : 1-58.

Caira JN, 1992. Verification of multiple species of *Pedibothrium* in the Atlantic nurse shark with comments on the Australasian members of the genus. Journal of Parasitology 78 : 289-308.

Caira JN, Burge AN, 2001. Three new species of *Acanthobothrium* (Cestoda : Tetraphyllidea) from the Ocellate Electric Ray, *Diplobatis ommata*, in the Gulf of California, Mexico. Comparative Parasitology 68 : 52-65.

Caira JN, Jensen K, 2001. An investigation of the co-evolutionary relationships between onchobothriid tapeworms and their elasmobranch hosts. International Journal for Parasitology 31 : 960-975.

Caira JN, Keeling CP, 1996. On the status of the genus *Pinguicollum* (Tetraphyllidea : Onchobothriidae) with a redescription of *P. pinguicollum*. Journal of Parasitology 82 : 463-469.

Caira JN, Pritchard MH, 1986. A review of the genus *Pedibothrium* Linton, 1909 (Tetraphyllidea : Onchobothriidae) with description of two new species and comments on the related genera *Pachybothrium* Baer and Euzet, 1962 and *Balanobothrium* Hornell, 1912. Journal of Parasitology 72 : 62-70.

Caira JN, Rasolofonirina R, 1998. A new species of *Pedibothrium* (Cestoidea : Tetraphyllidea) from the short-tail nurse shark, *Pseudoginglymostoma brevicaudatum* (Elasmobranchii : Orectilobiformes) from southwest Madagascar. Journal of the Helminthological Society of Washington 65 : 50-55.

Caira JN, Ruhnke TR, 1990. A new species of *Calliobothrium* (Tetraphyllidea : Onchobothriidae) from the whiskery shark, *Furgaleus macki*, in Australia. Journal of Parasitology 76 : 319-324.

Caira JN, Zahner SD, 2001. Two new species of *Acanthobothrium* Beneden, 1849 (Tetraphyllidea : Onchobothriidae) from horn sharks in the Gulf of California, Mexico. Systematic Parasitology 50 : 219-229.

Chabaud A, 1982. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés, 13-17 Avril, 1981. Mémoires du Muséum National d'Histoire Naturelles (Nouvelle Séries). Série A, Zoologie 123 : 1-326.

Chisholm LA, Morgan JAT, Adlard RD, Whittington ID, 2001. Phylogenetic analysis of the Monocotylidae (Monogenea) inferred from 28S rDNA sequences. International Journal for Parasitology 31: 1253-1263.

Clayton DH, Price RD, 1998. Taxonomic review of Cotingacola (Phthiraptera : Philopteridae) from the cotingas (Passeriformes : Tyrannidae), with descriptions of two new species. Journal of Medical Entomology 35 : 732-739.

Clements JF, 2000. Birds of the World : A Checklist. Ibis Publishing Company, Vista, California, USA : 867 p.

Combes C, 2001. Parasitism. The Ecology and Evolution of Intimate Interactions. University of Chicago Press, Chicago, USA : 728 p.

Cumming GS, 1998. Host preference in African ticks (Acari : Ixodida) : a quantitative data set. Bulletin of Entomological Research 88: 379-406.

Dusek L, Gelnar M, Sebelová S, 1998. Biodiversity of parasites in a freshwater environment with respect to pollution : Metazoan parasites of chub (*Leuciscus cephalus* L.) as a model for statistical evaluation. International Journal for Parasitology 28: 1555-1571.

Erwin TL, 1982. Tropical forests : their richness in Coleoptera and other arthropod species. The Coleopterist's Bulletin 36 : 74-75.

Esch GW, Fernández JC, 1993. A Functional Biology of Parasitism. Chapmen and Hall, London, UK : 337 p.

Euzet L, Combes C, 1980. Les problèmes de l'espèce chez les animaux parasites. In : Les problèmes de l'espèce dans le règne animal. Mémoires de la Société Zoologique de France 3 : 239-285.

Fain A, 1994. Adaptation, specificity and host-parasite coevolution in mites (Acari). International Journal for Parasitology 24 : 1273-1283.

FishBase (www.fishbase.org), 2002. Froese R, Pauly DE, editors. March 2002, World Wide Web electronic publication.

Ghoshroy S, Caira JN, 2001. Four new species of *Acanthobothrium* (Cestoda : Tetraphyllidea) from the whiptail stingray *Dasyatis brevis* in the Gulf of California, Mexico. Journal of Parasitology 87 : 345-372.

Gibson DI, 1996. Trematoda. In : Margolis L, Kabata Z, editors. Guide to the Parasites of Fishes of Canada. Part IV. Canadian Special Publication of Fisheries and Aquatic Sciences 124 : 1-373.

Hargis WJ Jr, 1957. The host specificity of monogenetic trematodes. Experimental Parasitology 6 : 610-625.

Healy CJ, Scholz T, Caira JN, 2001. *Erudituncus* n. gen. (Tetraphyllidea : Onchobothriidae) with a redescription of *E. musteli* (Yamaguti, 1952) n. comb. and comments on its hook homologies. Journal of Parasitology 87 : 833-837.

Holmes JC, 1990. Helminth communities in marine fishes. In : Esch GW, Bush AO, Aho JM, editors. Parasite Communities : Patterns and Processes. Chapman and Hall, New York, USA : 101-130.

Hoogstraal H, Aeschlimann A, 1982. Tick-host specificity. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés, 13-17 Avril, 1981.

Mémoires du Muséum National d'Histoire Naturelles (Nouvelle Séries). Série A, Zoologie 123 : 157-171.

Kennedy MJ, Newman RA, 1986. Synopsis of the Parasites of Vertebrates of Canada. Ectoparasites of Terrestrial Mammals. Alberta Agricultural Animal Health Division : 109 p.

Kim KC, 1982. Host specificity and phylogeny of Anoplura. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés, 13-17 Avril, 1981. Mémoires du Muséum National d'Histoire Naturelles (Nouvelle Séries). Série A, Zoologie 123 : 123-127.

Klompen JSH, Black WC, Keirans JE, Oliver, JI, 1996. Evolution of ticks. Annual Review of Entomology 41 : 141-161.

Lambert A, 1982. Spécificité parasitaire et évolution des Monogenea Monocotylidae, Platyhelminthes parasites de sélaciens. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés, 13-17 Avril, 1981. Mémoires du Muséum National d'Histoire Naturelles (Nouvelle Séries). Série A, Zoologie 123 : 303-311.

Lindblad I, 2000. Host specificity of some wood-inhabiting fungi in a tropical forest. Mycologia 92 : 399-405.

Llewellyn J, 1957. Host-specificity in monogenetic trematodes. Premier Symposium sur la spécificité parasitaire des parasites de vertébrés. Insitut de Zoologie, Université de Neuchâtel, Suisse : 199-212.

Llewellyn J, 1982. Host specificity and corresponding evolution in monogenean flatworms and vertebrates. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés, 13-17 Avril, 1981. Mémoires du Muséum National d'Histoire Naturelles (Nouvelle Séries). Série A, Zoologie 123 : 289-293.

Love MS, Moser M, 1983. A checklist of parasites of California, Oregon, and Washington marine and esturine fishes. NOAA Technical Report, NMFS SSRF-777 : 1-576.

Ludwig HW, 1982. Host specificity in Anoplura and coevolution of Anoplura and Mammalia. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés, 13-17 Avril, 1981. Mémoires du Muséum National d'Histoire Naturelles (Nouvelle Séries). Série A, Zoologie 123 : 145-152.

Lymbery AJ, 1989. Host specificity, host range and host preference. Parasitology Today 5 : 298.

Margolis L, Arthur JR, 1979. Synopsis of the Parasites of Fishes of Canada. Bulletin of the Fisheries Research Board of Canada 199 : 1-269.

Marshall AG, 1981. The Ecology of Ectoparasitic Insects. Academic Press, London, UK : 459 p.

Mawdsley NA, Stork NE, 1997. Host-specificity and the effective specialization of tropical canopy beetles. In : Stork NE, Adis J, Didham RK, editors. Canopy Arthropods. Chapman and Hall, London, UK : 104-130.

May RM, 1979. Patterns in the abundance of parasites on plants. Nature 281 : 425-426.

May R, 1990. How many species ? Philosophical Transactions. Biological Sciences 330 : 293-303.

Moss WW, 1979. Patterns of host-specificity and co-evolution in the Harpyrhynchidae. Advances in Acarology 2 : 379-384.

Moss WW, Wojcik JF, 1978. Numerical taxonomic studies of the mite family Harpyrhynchidae (Acari : Cheyletoidea) : the higher taxa. Annals of the Entomological Society of America 71 : 247-252.

Nasin CS, Caira JN, Euzet L, 1997. Analysis of *Calliobothrium* (Tetraphyllidea : Onchobothriidae) with descriptions of three new species and erection of a new genus. Journal of Parasitology 83 : 714-733.

Noble ER, Nobel GA, Schad GA, MacInnis AJ, 1989. Parasitology. The Biology of Animal Parasites. Sixth Edition. Lea and Febiger, Philadelphia, USA: 574 p.

Nowak RM, 1991. Walker's Mammals of the World. Fifth Edition. Volume I & II. Johns Hopkins University Press, Baltimore, USA : 1629 p.

Ødegaard F, 2000. How many species of arthropods ? Erwin's estimate revised. Biological Journal of the Linnean Society 71 : 583-597.

Olson PD, Caira JN, 2001. Two new species of *Litobothrium* Dailey, 1969 (Cestoda : Litobothriidae) from thresher sharks in the Gulf of California, Mexico, with redescriptions of two species in the genus. Systematic Parasitology 48 : 159-177.

Podlipaev S, 2001. The more insect trypanosomatids under study- the more diverse Trypanosomatidae appear to be. International Journal for Parasitology 31 : 748-752.

Poinar JR Jr, 1979. Nematodes for Biological Control of Insects. CRC Press, Inc., Boca Raton, Florida, USA : 277 p.

Poulin R, 1992. Determinants of host-specificity in parasites of freshwater fishes. International Journal for Parasitology 22 : 753-758.

Poulin R, 1997. Parasite faunas of freshwater fish : The relationship between richness and the specificity of parasites. International Journal for Parasitology 27 : 1091-1098.

Price PW, 1980. Evolutionary biology of parasites. Monographs in Population Biology 15 : 3-237.

Rohde K, 1978. Latitudinal differences in host-specificity of marine Monogenea and Digenea. Marine Biology 47 : 125-134.

Rohde K, 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. American Naturalist 114 : 648-671.

Rohde K, 1980. Host specificity indices of parasites and their applications. Experientia 36 : 1370-1371.

Rohde K, Heap M, 1998. Latitudinal differences in species and community richness and community structure of metazoan endo- and ectoparasites of marine teleost fish. International Journal for Parasitology 28 : 461-474.

Sandground JH, 1929. A consideration of the relation of host-specificity of helminths and other metazoan parasites to the phenomena of age resistence and aquired immunity. Parasitology 21: 227-255.

Sasal P, Trouvé S, Müller-Graf C, Morand S, 1999. Specificity and host predictability : a comparative analysis among monogenean parasites of fish. Journal of Animal Ecology 68 : 437-444.

Steinlein DB, Burden LA, Cannon WL, 2001. Tick (Acari) infestations of bats in New Mexico. Journal of Medical Entomology 38 : 609-611.

Stevens PF, 2001 onwards. Angiosperm Phylogeny Website. Version 2 August 2001. http://www.mobot.org/MOBOT/research/APweb.

Telford SR, Wozniak EJ, Butler JF, 2001. Haemogregarine specificity in two communities of Florida snakes, with descriptions of six new species of *Hepatoxo on* (Apicomplexa : Hepatozoidae) and a possible species of *Haemogregarina* (Apicomplexa : Haemogregarinidae). Journal of Parasitology 87 : 890-905.

Van As JG, Basson L, 1987. Host specificity of trichodinid ectoparasites of freshwater fish. Parasitology Today 3 : 88-90.

Williams RB, 1986. Host specificity of avian Coccidia. Parasitology Today 2 : 283-284.