Acanthocephala in *The Journal of Parasitology*, 1914–2014

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The launch of *The Journal of Parasitology* (*JP*) by Henry Baldwin Ward in September 1914 was a historical landmark that witnessed the passage of the torch of acanthocephalan work, especially higher taxonomy, from Europe to the United States, with the excep-tion of the works of Anton Meyer, Yves Golvan, and a few Russian workers in the early twentieth century. At that juncture, there were only two primary English-language parasitological journals, i.e., *The Journal of Parasitology* and *Parasitology*. Research then was optical microscopy-based taxonomy work. There are now more than 30 parasitology-based journals with multiple sub-specialties because of rapidly advancing technologies. Advances in molecular and gene sequenc-ing techniques, especially over the last two decades, have helped resolve many taxonomic and evolutionary questions.

The present paper is thematic and will address the *JP* contributions to resolving taxonomic, evolutionary, biological, behavioral, and related issues posed by the acanthocephalan challenge as models for parasitological research. The most notable observation is that taxo-nomic studies of Acanthocephala, whether such work utilized classical or molecular approaches, has been one of the most solid and consistent fields of study over the years. Life cycle, behavioral, seasonal, developmental, and related studies, like fads, seem to last for a few decades before they fade away, and are replaced by new approaches. Changes of emphasis, as well as progressive developments in technology, especially in the areas of gene sequencing, molecular, and evolutionary biology, account for most of these trends that also reflect world-wide patterns of intellectual interest. The two taxonomy sections below incorporate *JP* as well as other journal sources. All subsequent sections address only *JP* articles.

Classical taxonomy

Classical taxonomy articles were the most commonly published research on Acanthocephala in *JP* during its 100 years of existence. The first number of *JP* included Van Cleave's (1914) proposal of *Eorhynchus* (Hamann, 1892), now *Neoechinorhynchus* Stiles and Hassall, 1905, as a new name for *Neorhynchus* (Hamann, 1892).

Harley J. Van Cleave, the "father" of acanthocephalan taxonomy in the US, picked up where the European masters left off. Rudolphi (1802) was the first to name these worms Acanthocephala and gave them an ordinal rank, with one genus, *Echinorhynchus*. Most early taxonomic works lacked detailed morphological information until Lühe's (1904, 1905) critical reviews of the early descriptions. Hamann (1892) recognized the diversity of this group of worms and split the old genus *Echinorhynchus* into three families (Echinorhynchidae, Gigantorhynchidae, Neorhynchidae), an action that formed a basis for later classifications of Acantho-cephala. These divisions were subsequently elevated to ordinal rank by Meyer (1931) and Van Cleave

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(1936), but only to subordinal rank by Southwell and MacFie (1925), among taxonomic variations proposed by other observers, including Travassos (1926), Thapar (1927), Witenberg (1932a, 1932b), and Meyer (1931, 1932, 1933).

Uncertainty about the position of Acanthocephala among other animal groups was marked by Leuckart's (1848) speculation of lines of descent between the cestodes and acanthocephalans, groups he placed as two orders in his class Anenteraeti, whereas Meyer (1932, 1933) regarded Acanthocephala as a class of the Aschelminthes that included two orders, Palaeacanthocephala and Archiacanthocephala based on morphology and ontogeny. Van Cleave (1936) removed the inconsistencies of Meyer's system by establishing a third order**,** Eoacanthocephala. He also recognized Acanthocephala as a phylum (Van Cleave 1941, 1948), closely associated with the Cestoda.

More recently, Petrochenko (1956) devised a system based heavily on acanthor spination. Golvan (1959, 1960, 1961, 1965, 1969, 1994) considered Eoacanthocephala (now regarded as the most ancient group), Palaeacanthocephala, and Archiacanthocephala to be classes, relying heavily on the number of cement glands and on trunk spination. Yamaguti (1963) recognized three orders, namely, Neoechinorhynchidea, Echinorhynchidea, and Gigantorhynchidea, corresponding to the Meyer–Van Cleave classes, as well as a new fourth order, Apororhynchidea. Golvan's (1994) nomenclature of the Acanthocephala was a culmination of his life-long contributions to the systematics of this phylum (Amin, 2013).

The standard classification of the Acanthocephala provided by Amin (1985), and an earlier synopsis (Amin, 1982), were updated to include hierarchal changes and a considerable number of new taxa (Amin, 2013). This latest classification continued to retain its affiliation with the systems of Meyer (1931, 1932, 1933) and Van Cleave (1936, 1941, 1947, 1948, 1949, 1951, 1952), but incorporated new contributions of molecular taxonomy and phylogenetic studies to the taxonomic system. The recognition of a new order, Neoacanthocephala (now Neoechinorhynchidae; Southwell and MacFie, 1925) (Van Cleave, 1936), the treatment of the Eoacantho-cephala of North America (Van Cleave, 1947), and Van Cleave's (1948) expansions of the phylum Acan-thocephala were landmark contributions that were originally published in *JP*. These quoted workers did exactly what modern molecular taxonomists are doing, but with a different set of tools. They considered individ-ual species and lower taxa as models for higher patterns and trends to which these groups needed to be assigned in order to resolve the larger evolutionary picture.

Taxonomy in the highest sense is a science of relationships. Taxonomists dealing with higher taxa see their world in a gestalt perspective. Regrettably, modern systematists, the molecular taxonomists included, often see the leaves and, at best the small branches, but do not see the trunk and the roots of the classification system. Just because the roots are buried in the darkness of the earth does not mean that they are not there. Higher tax-onomy has faded away with the passing of the masters who had great vision and were not encumbered by the limitations of the optical tools. Having a taxonomically based Ph.D. in parasitology or publishing a new species here and there is not the same as really practicing tax-onomy. One can spend a lifetime classifying crabs based on differences in their neurological systems, but at the end of the day, one still does not really know the crab, or the shore, or the ocean. It is in these more inclusive relationships that higher taxonomy belongs.

There are many world-class taxonomists who have described a substantial number of species or genera of Acanthocephala over the years. Because of space limitations, it will not be possible to list all the authors and associated descriptions published over a 100-year period. However, such a list is available in Amin's (2013) classification, with an index to families and genera. Authors of descriptions of lower taxa published in *JP*, since 1914, are herein included in chronological order based on first appearance: H. J. Van Cleave, D. R. Lincicome, E. M. Pratt, A. C. Chandler, M. L. Perry, H. L. Ward, M. A. Tubangui, V. A. Masilun-gan, H. W. Manter, J. D. Webster, E. E. Byrd, J. F. Denton, E. C. Haderlie, R. B. Williams, H. F. Timmons, L Sarmiento, R. M. Cable, W. B. Hopp, L. Margolis, W. L. Bullock, E. N. Das, F. M. Fisher, Jr., K. A. Neiland, G. D. Schmidt, J. Linderoth, F. L. Dunn, R. M. Laurs, J. E. McCauley, R. E. Kuntz, D. R. Nelson, B. B. Nickol, L. M. Cordonnier, F. E. Kellogg, V. E. Thatcher, E. J. Hugghins, A. M. Dunn, G. Samuel, O. M. Amin, E. H. Williams, D./ F. Oetinger, R. L. Buckner, S. C. Buckner, I. Paperna, D. G. Huffman, T. N. Padilha, S. H. Loetta, A. A. Kocan, B. Marchand, G. Vassiliades, H. L. Ching, W. A. Rogers, T. P. Deveaux, M. Krishnasamy, L. R. Smales, S. J. Edmonds, N. P. Boyce, R. A. Heckmann,

N. V. Ha, A. M. El-Naggar, O. N. Bauer, E. G. Sidorov, S. Ortubay, C. Ubeda, L. Semenas, C. R. Kennedy, J. A. Ewald, D. W. T. Crompton, F. M. Nahhas, J. F. Munro, R. C. Stoddart, B. S. Dezfuli, S. Monks, D. Bolette, D. W. Searle, G. Munoz, M. George-Nascimento, G. Salgado-Maldonado, A. Cruz-Reyes, S. Monks, G. Pulido-Flores, C. R. Bursey, S. Goildberg, F. Thielen, M. Muenderle, H. Tarascheeski, B. Sures, M. Garcia-Varela, G. Perez-Ponce- de Leon, F. J. Aznar, S. Nadler, A. L. Lanfranchi, O. L. Lisitsyna, V. V. Tkach, S. A. Bush, Z Gholami, M. Akhlaghi, A. Maria Santana-Pineros, Y. Cruz-Quintana, O. Arturo Centeno-Chale, V. M. Vidal-Martinez, D. Vrcibradic, F. H. Hatano, C. F. D. Rocha, V. L. Olmos, E. M. Habit, N. A. Radwan, J. S. Mantuano Anchundia, M. A. Zambrano Alcivar, F. M. Vieira, N. N. Felizardo, J. L. Luque, D. W. Duszynski, A. Halajian, A. Eslami, J. T. Timi, and C. A. Fuller.

(Editors' note: This list is a truly remarkable one that includes a very diverse group of scientists from around the world, not only people who have made an intellectual career studying Acanthocephala, but also those whose main research interests have been with other groups. A Google® or library database search on these names, for example using online Biological Abstracts, would be a major lesson in the history of parasitology, the way in which interest and opportunity drive investigations, and the impact that curiosity has on a scientist's life. We thank Dr. Amin for compiling this list!)

Contributors to the higher taxonomy of Acanthocephala who also dealt with generic and supra-generic taxa include G. D. Schmidt and collaborators, D. J. Richardson, L. R. Smales, and O. M. Amin. Schmidt and Neiland (1966) revised the helminth fauna of Nicaragua and described new centrorhynchid species, while Schmidt and Kuntz (1967a) revised the Porrorchinae and described new genera and species. Schmidt (1972) revised the class Archiacanthocephala Meyer, 1931. Schmidt and Hugghins (1973a, 1973b) revised the Eoacanthocephala and the Palaeacanthocephala of South American fishes, respectively. Richardson and Nickol (1995) revised the genus *Centrorhynchus* in North America and Smales (2002) examined species of *Mediorhynchus* Van Cleave, 1916 in Australian birds.

Amin's contributions included the classification of the Acanthocephala (Amin, 1982, 1985, 2013), the erection of a new class, Polyacanthocephala, with keys to acanthocephalan families and subfamilies (Amin, 1987), a review of *Polymorphus*, including synonymization of previously described species from other genera (Amin, 1992), review of Acanthocephala of the Neotropical region (Amin, 2000), a revision of *Neoechinorhynchus*; Stiles and Hassall, 1905, with the erection of two new subgenera, *Neoechinorhynchus*; Hamann, 1892, and *Hebe-soma*; Van Cleave, 1928 (Amin, 2002), and the erection of a new acanthocephalan order (Heteramorphida; Palaeacanthocephala) and family (Pyrirhynchidae) that is intermediate between Polymorphidae and Heteracanthocephalidae, and parasitic in birds in Vietnam (Amin and Ha, 2008). Amin (2000) listed and annotated the Acanthocephala in the Neotropical region. In an obscure publication, Bhattacharya (2007) listed 251 acanthocephalan species from India and described a few species and genera, but did not recognize the Neoechinorhynchida; he also included its families in Gyracanthocephala. Salgado-Maldonado (2006) listed and discussed all helminth parasites of freshwater fishes in Mexico. Salgado-Maldonado and Amin (2009) followed with the acanthocephalan species of the Gulf of Mexico. Khatoon and Bilqees (2011) then published an expanded version of their conventional classification from 1991, but their work included a number of errors and misplacements of higher taxa.

Molecular-evolutionary taxonomy

Advances in molecular and gene sequencing techniques, especially during the last two decades, have helped resolve many taxonomic and evolutionary questions. This work dealt with a number of questions of long standing and provided a new set of answers from different perspectives. These studies include the following contributions as reviewed in Amin (2013). Meyer (1932, 1933) grouped the Acanthocephala with the Rotifera, Gastrotricha, Kinorhyncha, Priapuloidea, Nematomorpha, and Nematoda within the phylum Aschelminthes. Recent molecular studies by Garey et al. (1996), García-Varela et al. (2000), Welch (2000), and Near (2002), among others, even suggest that Rotifera and Acanthocephala are phylogenetically related sister groups. Garey et al. (1996) asserted that the Acanthocephala represent a taxon within phylum Rotifera. Several workers have since demonstrated the sister group relationship of Acanthocephala with Rotifera, forming a new phylum, Syndermata Ahlrichs, 1997. In an extension of these findings, Garey et al. (1998), Zrzavý (2001), Kristensen (2002), García-Varela and Nadler (2006), Witek et al. (2008), Fontaneto and Jondelius (2011) linked Gnathostomulida with Micrognathozoa and moved Syndermata into a larger clade, Gnathifera. The Gnathifera was first proposed by Rieger and Tyler (1995) and has been established as a monophyletic clade (Syndermata + Gnathostomulida) by Witek et al. (2009).

Phylogeny within the Syndermata subtaxon Acanthocephala was studied by sequencing the mitochondrial genomes of species from Palaeacanthocephala, Eoacanthocephala, Archiacanthocephala, and Bdelloidea, as well as of other syndermatans, 18 lophotrochozoan (spi-ralian) taxa, and one outgroup representative (Weber et al., 2013). Phylogenetic analyses have shown that the monophyletic Archiacanthocephala represented the sister taxon of a clade comprising Eoacanthocephala and the monophyletic Palaeacanthocephala. This topology suggests the secondary loss of lateral sensory organs (sensory pores) in Palaeacanthocephala and is in further agreement with the emergence of apical sensory organs in the stem lineage of Archiacanthocephala as defined by Weber et al. (2013).

Because acanthocephalans and tapeworms are without an intestine, the two groups have been considered as being related. Cholodkovsky (1897) was the first to propose such a relationship after Leuckart's (1848) early accounts; this view has been supported by Skrjabin and Shults (1931), Petrochenko (1952), Van Cleave (1941), and Amin et al. (2009). The latter authors identified what appear to be microtriches on the trunk epidermis of *Rhadinorhynchus ornatus* Van Cleave, 1918 (Rhadinorhynchidae) from skipjack tuna, *Katsuwonus pelamis* (Linnaeus), in the Pacific Ocean off South America. Another marine rhadinorhynchid acantho-cephalan, *Leptorhynchoides polycristatus*, from sturgeons in the Caspian Sea, appears to have similar structures (Amin et al., 2013). However, these structures may not be homologous with microtriches of cestodes; see Chervy (2009) for details regarding microtriches in cestodes.

According to Garey et al. (1998), combining molec-ular and morphological analyses of Bilateria leads to a tree with Platyhelminthes, Rotifera, Acanthocephala, and Gnathostomulida (and probably Gastrotricha) as a sister group to the annelid-mollusk lineage of the Spiralia (Lophotrochozoa). Steinauer et al. (2005), using mitochondrial (mt) genome sequences, suggested that Acanthocephala, as inferred from the mt genome of *Leptorhynchoides thecatus* (Linton, 1891), are closer to Platyhelminthes than was previously supposed. Their data are consistent with the data contained in numerous related studies based on RNA analysis. For instance, Min and Park (2009) linked Syndermata with Platyhelminthes as the Platyzoa. Under all proposals, monophyly of the major taxonomic groups of the Acanthocephala has been established (Near et al., 1998; Monks, 2001; Near, 2002), suggesting that the present classification of higher taxa is natural.

Many examples of molecular taxonomy of lower taxa leading to reassignments or to creation of higher taxa are included in Amin (2013). Ten instructive examples follow:

1 Distinguishing *Mediorhynchus africanus* Amin, Evans, Heckmann, El-Naggar, 2013 from the Asian *M. gallinarum* (Bhalerao, 1937) Van Cleave, 1947, was based on morphological evidence, SEM, and gene sequence analysis using DNA sequence from one mitochondrial gene (cytochrome oxidase subunit 1) and one nuclear gene, 18S rRNA, to infer the phylogenetic relationships of *M. africanus* and *M. gallinarum* and selected Acanthocephala. *Medioryhnchus* was shown to be monophyletic and *M. africanus* and *M. gallinarum* to be allopatric sister species with 9.7% sequence divergence.

2 Rosas-Valdez et al. (2012) presented phylogenetic trees for two known species of *Floridosentis* Ward, 1953. These authors showed that *Floridosentis* is monophyletic, and is comprised of two major, well-supported clades that correspond with the two noted species and their geographical distribution.

3 Salgado-Maldonado (2006) suggested the existence of two cryptic species within *Neoechinorhynchus (Neoechinorhynchus) golvani*, one associated with cichlids and the other with eleotrids in Mexico. Monks et al. (2011) subsequently described *N. (N.) brentnickoli* from eleotrid fishes. Martinez-Aquino

et al. (2009) revealed a complex of three cryptic species within *N. golvani* using two nuclear gene sequences that were associated with eleotrid and cichlid fish lineages in waters of different salinities.

4 The criteria for the classification of families of Palaeacanthocephala based on morphological characteristics may need to be re-evaluated using gene sequencing methods to establish phylogenetic relationships; for example, see García-Varela and Nadler (2005). Verweyen et al. (2011) analyzed 39 species from all four classes of Acanthocephala using nuclear 18S rDNAsequences. They found that the resulting trees suggested a paraphyletic arrangement of the Echinorhynchida and Polymorphida within the Palaeacanthocephala.

5 Väinölä et al. (1994) demonstrated strong allozyme divergence between the marine *Echinorhynchus gadi* (Zoega in Müller, 1776) Van Cleave, 1924, and the fresh-brackish-water *E. salmonis*, supporting the genetic distinction between these two taxa. Sobecka et al. (2012) compared populations of *E. gadi* from the Atlantic cod, *Gadus morhua* Linneaus, in the Baltic Sea and the North Atlantic morphometrically and genetically, using polymerase chain reaction restriction fragment length polymorphism and selected PCR products. Their analysis indicated that the nucleotide sequences of *E. gadi* rDNA from cod collected from all sites are identical. Morphometric analysis, however, demonstrated the separation of *E. gadi* into two groups, corresponding with the separation of cod into two subspecies, *G. m. morhue* in the Atlantic and *G. m. callarias* in the Baltic.

6 Tkach et al. (2013) used comparative analysis of nuclear ribosomal rRNA sequences encompassing the 3' end of 18S nuclear rDNA gene, internal transcribed spacer region (ITS 1+5.8S+ITS 2), and 5' end of the 28S gene to demonstrate significant differences between *Pseudoacanthocephalus nickoli* Tkach, Lisitsyna, Crossley, Binh, and Bush, 2013, and *P. smalesi* Tkach, Lisitsyna, Crossley, Binh, and Bush, 2013, as well as between these two species and closely related species from China and Vietnam.

7 Based on isoenzyme analysis, Dudinák and Šnábel (2001) described the genetic differences between the *Pomphorhynchus laevis* (Zoega in Müller, 1776) Van Cleave, 1924, populations of the Slovak and Czech Republics. Geographic isolation has evidently produced distinct genetic forms irrespective of host species. Perrot-Minnot (2004) demonstrated a high level of sequence divergence at ITS 1, ITS 2, and cytochrome c oxidase between smooth and wrin-kled cystacanths of *P. laevis*, molecular differences that corresponded with phototactile behavioral differences in gammarid hosts. She speculated that the smooth type corresponds to *P. laevis* and the wrinkled type to *P. tereticollis*, a former synonym of *P. laevis*. Špakulová et al. (2011) distinguished between *P. laevis* and *P. tereticollis* based on differences in proboscis armature and gene sequences using ITS 1, ITS 2, and CO1.

8 Aznar et al. (2006) split *Corynosoma* Lühe, 1904 (*fide* Van Cleave 1945) into two genera, *Corynosoma* for marine species and *Pseudocorynosoma* for freshwater species, based on anatomical, ecological, and phy-logenetic divergences. García-Varela et al. (2013) further demonstrated that *Pseudocorynosoma* species form an independent lineage that does not share a common ancestor with species of *Corynosoma* or *Andracantha*.

9 Amin's (1992) revision of *Polymorphus* Lühe, 1911, recognized two subgenera, *Polymorphus* Lühe, 1911, and *Profilicollis* Meyer, 1931. The elevation of these two subgenera to the generic level has been contro-versial, e.g., Nickol et al. (1999) supported it based on intermediate host affinities, but García-Varela and Pérez-Ponce de León (2008) disagreed based on sequences of the *cox 1* gene.

10 The validity of class Polyacanthocephala; Amin, 1987, was supported by ribosomal RNA gene sequence studies by García-Varela et al. (2002).

Parts of this discussion on taxonomy were adapted from Amin (1985, 2013).

Lessons learned from the history of acanthocephalan taxonomy

Molecular and gene sequencing techniques are elegant tools that help to distinguish the identity of newly described taxa from related ones, confirm the lineages and assignment of higher taxa using character states of evolutionary significance, and establish relation-ships among higher taxa that may be in agreement or disagreement with previously proposed ones based only on morphological grounds. It is to be expected that genotypic distinctions may not be sufficient alone and that phenotypic assignments can, and do, still carry considerable weight.

Life cycles

Life cycle studies were the second most commonly reported in *JP*, especially during the 1960s. Like fads, they gradually declined until they came to a virtual stop by the end of the 1980s. Van Cleave's studies of the life cycles of *Echinorhynchus coregoni* Linkins in Van Cleave, 1919, and *Leptorhynchoides thecatus* (Linton, 1891) Kostylew, 1924, inaugurated this field of study in the 1920s. De Giusti (1939, 1949) provided more detailed life cycle studies of *L. thecatus* in the 1930s and 1940s. Moore (1946) added similar information regarding *Macracanthorhynchus ingens* Meyer, 1933. Reish (1950) later reported on the life cycle of *Profilicollis altmani* (Perry, 1942) Van Cleave, 1947 (= *Polymorphus kenti* Van Cleave, 1947); Hopp (1954) for *Neoechinorhynchus emydis* (Leody, 1851) Van Cleave, 1919, (*nec* 1916); Moore (1962) for *Mediorhynchus grandis* Van Cleave, 1916: Merriott and Pratt (1964) for *Neoechinorhynchus rutili* (Müller, 1780); Schmidt and Olson (1964) for *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966 (= *Prosthorhynchus formosus* (Van Cleave, 1918) Travassos, 1926); and Harms (1965) for *Octospinifer macilentis* Van Cleave, 1919.

The life cycle of *Prosthenorchis elegans* (Diesing, 1851) Travassos, 1915, was reported by Stunkard (1965; Stoddart, 1965), that of *Profilicollis formosus* by Schmidt and Kuntz (1967a), and that of *Paulisentis fractus* Van Cleave and Bangham, 1949, by Cable and Dill (1967); and Uglem and Larson (1969) for *Neoechinorhynchus saginatus* Van Cleave and Bangham, 1949. The life cycles of three polymorphids, *Corynosoma constrictum* Van Cleave, 1918, *Polymorphus contortus* (Bremser, 1821) Travassos, 1926, and *P. trochus* Van Cleave, 1945, and their development in *Hyalella azteca* Saussure, 1858, were reported by Podesta and Holmes (1970). Olson and Pratt (1971) reported the life cycle and larval devel-opment of *Echinorhynchus lageniformis* Ekbaum, 1938. Uglem (1972) studied the life cycle of *Neoechinorhynchus cristatus* Lynch, 1936, and provided information on the hatching of eggs. Nickol (1977) discussed the life history and host specificity of *Mediorhynchus centurorum* Nickol, 1969; Samuel and Bullock (1981) for *Paratenuisentis ambiguus* (Van Cleave, 1921) Bullock and Samuel, 1975; De Mont and Corkum (1982) for *Octospiniferoides chandleri* Bullock, 1957; and Brattey (1988) and by Benesh and Valtonen (2007) for *Acanthocephalus lucii* (Müller, 1776) Lühe 1911.

Lessons learned from the study of acanthocephalan life cycles

Life cycle studies are valuable not only for the understanding of the metamorphosis of specimens of studied species and their host and environmental relationships (if not studied only under laboratory conditions), but also for other reasons. Most species of acanthocephalans are described from the adult stages and some are known only from immature specimens. In both situations, the relationship between the taxonomic characters in specimens of each of the two stages remains unknown. For example, trunk, proboscis or lemniscus form, position of the gonopore, patterns of trunk spination, hook, and hook root development in mature and immature forms often vary. Life cycle studies, including good morphometrics, would resolve questions of the assignment of mature and immature stages to the same or other species.

Behavioral studies

Behavioral studies reported in *JP*, especially of crustacean intermediate hosts infected with larval acanthocephalans, were also popular for a while, after a late start. These studies appear to have been a fashion that lasted about 20 years between the 1970s and the 1990s, and have since faded away. Bowen (1967) observed defense reactions in millipedes infected by larval *M. ingens*. Bethel and Holmes (1973, 1974) correlated the evasive behavior and responses to light of *Gammarus lacustris* Sars, 1864, infected with *Polymorphus paradoxus* Connel and Corner, 1957, with promoting infection in the definitive host. Altered color, behavior, and predation susceptibility of the isopopod, *Asellus intermedius* Forbes, 1876, infected with *Acanthocephalus dirus* (Van Cleave, 1931) Van Cleave and Townsend, 1936, were reported by Camp and Huizinga (1979). Oetinger and Nickol (1982a, 1982b) examined the spectrophotometric characteristics of the integument pigments of *A. intermedius* and the developmental relationships with *A. dirus*.

Moore (1983) and Moore and Gottelli (1992) examined the altered behavior in two species of cockroaches infected with *Moniliformis moniliformis* (Bremser, 1811) Travassos, 1915. Later, Carmichael and Moore (1991) compared the altered behavior in the brown cockroach and the American cockroach infected with *M. moniliformis*, but Allely et al. (1992) showed that infections with *M. Moniliformis* had no behavioral effects on the viviparous pacific cockroach *Diploptera punctata* (Eschscholtz). Zhao and Wang (1992) examined the defense reaction against the larvae of *Macracanthorhynchus hirudinaceus* (Pallas, 1781) Travas-sos, 1917, in laboratory-infected beetles. Freehling and Moore (1993) established the susceptibility of 13 species of cockroaches to infections with *M. moniliformis*. Moore et al. (1994) described the altered behavior of two species of blattid cockroaches infected with *M. moniliformis*. Moore and Gotelli (1996) explored the evolutionary patterns of altered behavior and susceptibility in parasitized hosts.

Maynard et al. (1998) studied the altered behavior of the amphipod *Echinogammarus stammeri* Karaman, 1931, infected with *Pomphorhynchus laevis* (Zoega in Müller, 1776) Van Cleave, 1924. Benesh et al. (2005) studied behavioral response to light by amphipods infected with *Corynosoma constrictum* Van Cleave, 1918. Benesh and Valtonen (2007) studied the effect of *Acan-thocephalus lucii* (Müller, 1776) Lühe, 1911, infections on intermediate host growth and survival. Benesh et al. (2008) observed the effect of *Echinorhynchus cinctulus* (Porta, 1905) Amin, 2013 (= *Echinorhynchus borealis* von Linstow, 1901) on anti-predator behavior of the amphi-pod intermediate host. The behavior of some vertebrate animals is also affected by acanthocephalans. Thus, McLennan and Shires (1995) were able to correlate the intensity of brook stickleback behavior with level of infection with *Neoechinorhynchus rutili* (Müller, 1780).

Lessons learned from the behavioral studies

Altered behavior involving color changes, behavioral alteration, and increased predation susceptibility of lar-val stages of acanthocephalans are rather commonplace in both aquatic and terrestrial systems. Accordingly, worms reach definitive hosts more effectively and in larger numbers than they would be able to otherwise, evidently leading to parasite survival at a low, or no, energy cost. These cases are excellent examples of strategies by which these parasites are assumed to insure their evolutionary success.

Ecological, seasonal and geographical distribution, and host-parasite relationships

This section has a wider, but related**,** coverage in *The Journal of Parasitology*. The first of these sorts of studies was by Van Cleave (1916), who reported the seasonal distribution of *Neoechinorhynchus emydis* (Leidy, 1851) Van Cleave, 1919 (*nec* 1916), *Gracilisen-tis gracilisentis* (Van Cleave, 1913) Van Cleave, 1919 (= *Neoechinorhynchus gracilisentis* Van Cleave, 1913), and *Tanaorhampus longirostris* (Van Cleave, 1913) Ward, 1918 (= *Neoechinorhynchus longirostris* (Van Cleave, 1913) Van Cleave, 1916). Thirty five years later, Fischthal (1950) reported on the geographic and host distribution of *Leptorhynchoides thecatus*. It took another 17 years for the ecology of *N. rutili* to be published by Walkey (1967).

The 1970s and 1980s appear to have been a reasonably good period for ecological/seasonal studies, but those have dwindled considerably in the twenty-first century. Seidenberg (1973) studied the ecology of *Acanthocephalus dirus* in its isopod intermediate host, *Asellus intermedius*. Amin (1975, 1986, 1987) examined the host and seasonal distribution of *A. dirus* (= *Acanthocephalus parksidei* Amin, 1975), of species of *Neoechinorhynchus* Stiles and Hassall, 1905, and of *Pomphorhynchus bulbocolli* Linkins in Van Cleave, 1919, respectively, in Wisconsin lakes. Muzzall and Bullock (1978) reported the seasonal and host-parasite relationships of *Neoechinorhynchus saginatus* in *Semotilus corporalis* (Mitchell). The seasonal occurrence and host specificity of *Gracilisentis gracilisentis* and *Tanaorhampus longrostris* in an Illinois lake were reported by Jilek (1978). Buckner and Nickol (1979) studied the geographic and host-related variation among species of *Fessisentis* Van Cleave, 1931. Muzzall (1980) explored the ecology and seasonal abundance of three acanthocephalan species infecting white suckers in New Hampshire. Camp and Huizinga (1980) studied the seasonal population interactions of *A. dirus* in *Semotilus atromaculatus* Mitchill, 1818 and *A. intermedius*. Elkins and Nickol (1983) studied the epizootiology of *M. ingens* in Louisiana. Gleason (1987) studied the population dynamics of *P. bulbocolli* in *Gammarus pseudolimnaeus* Bousfield, 1958. Ashley and Nickol (1989) examined the dynamics of *L. thecatus* suprapopulation in a Great Plains reservoir. Stoddart et al. (1991) examined the influence of host strain and helminth isolate on the relationship between rats and *M. moniliformis*.

Moser and Hsieh (1992) investigated biological tags for stock separation in Pacific herring. Trejo (1992) examined the host–parasite relationship of *Pom-phorhynchus patagonicus* Ortubay, Ubeda, Semenas and Kennedy, 1991, in two species of fish from Argentina. Olson and Nickol (1996) compared recruitment of *L. thecatus* in green sunfish and largemouth bass. Steinauer et al. (2006) examined the geographic and host use of *L. thecatus* in the U.S. Rauque et al. (2006) observed the seasonal recruitment and reproduction of *A. tumescens* in fishes from Argentina. Balboa et al. (2009) examined the distribution of cystacanths of two *Profilcollis* species in sympatric crustacean hosts in Chile. Rauque and Semanas (2011) used parasite volume as an indicator of competition between *Acanthocephalus tumescens* (von Linstow, 1896) Porta, 1905, and *Pseudo-corynosoma* sp. in their intermediate host. Kopp et al. (2011) and Wahl and Sparkes (2012) reported on the dispersal of *A. dirus* in the U.S.

Lessons learned from ecological studies on acanthocephalans

Ecological, geographical, and host-parasite specificity and relationships are currently being recognized as important variables embodying character states critical for the creation of phylogenetic trees addressing tax-onomic issues. It is no small feat that these variables can, and do, affect the taxonomy and evolution of the Acanthocephala directly or indirectly. As distinct as these areas of study may seem, they are actually connected in an integrated way. Throughout the last 50 years, life history and behavioral studies have been effectively used to answer ecological questions. They are not as expensive to execute as molecular work, and yield academic recognition and frequent publications. It is not surprising that the chronology of the high activity and decline of these studies followed the same pattern, fading away at the same time in the 1980s and 1990s. This decline also corresponded with the advent of new technology and molecular techniques that are regarded by some as better ones for answering some of the age-old questions. It is likely that in the near future, editors will require gene sequencing for new species descriptions.

It is inescapable to conclude that behavioral, life history and ecological questions can sometimes be addressed using molecular techniques. Molecular ecol-ogy is an emerging science addressing the role of genetic constitutions in the ecological and host parasite distribution. While sequencing may not provide the complete answer to the larger ecological or behavioral questions, it can shed light on some of these larger questions especially those involving evolutionary components.

Anatomy and ultrastructure

Anatomical studies published in *JP* also had a late start in the 1950s, blossomed in the 1970s and 1980s, and dwindled to a virtual end by the early 1990s. Ultrastructural studies became popular with the advent of technological advances. Electron microscopy is not regarded as particularly sophisticated nowadays, especially when compared to molecular approaches and related emphasis preferred by many journals and editors. Nonetheless, ultrastructural studies have made major contributions to our understanding of parasite biology. Examples of such research follow. Chromo-somes of *M. hirudinaceus* were described by Jones and Ward (1950) and Robinson (1964), and those of *M. moniliformis* by Robinson (1965). West (1964) demon-strated the presence of acanthor membranes in two species of Acanthocephala. Wright and Lumsden (1968, 1969) described the ultrastructural and histochemical properties of the acanthocephalan epicuticle, and of the pore canal system of *M. moniliformis*. Robinson (1973) described the growth and differentiation of giant nuclei in *M. Monilifomis*. Bone (1974) studied the chromosomes of *Neoechinorhynchus cylindratus* (Van Cleave, 1913) Van Cleave, 1919, and *L. thecatus*.

Dunagan and Miller (1976, 1978) described the cerebral ganglion and the genital ganglion of *M. moniliformis*, respectively. Schmidt (1977) described the praesomal musculature of acanthocephalan genus *Mediorhynchus* (Van Cleave, 1916). Miller and Dunagan (1978) and Dunagan and Miller (1981) described the lacunar system and the cerebral ganglion of *Oligacanthorhynchus tortuosa* (Leidy, 1850, Schmidt, 1972, respectively). Hutton and Oetinger (1980) demonstrated the morphogenesis of proboscis hooks of *M. moniliformis* Miller and Dunagan

(1983) and Dunagan and Miller (1983) described a support cell to the sensory organs and the apical sense organs of *M. hirudinaceus*, respectively. Marchand (1984) studied the ultrastructure of acanthor shells of 13 species of acanthocephalans. Budziakowski and Mettrick (1985) described the neuropile of the cerebral ganglion of *M. moniliformis*.

Dunagan and Miller (1985) also described the reproductive apparatus of *N. cylindratus* and the protonephridia in male *M. hirudinaceaus*. These same authors (Dunagan and Miller, 1986, 1987) described the sense organs of *M. moniliformis* using SEM, reviewed the protonephridia in Acanthocephala, and provided a model of the cerebral ganglion in *M. hirudinaceus*. Krapf and Dunagan (1987) and Dunagan and Bozzola (1989, 1992) described the structure of the protonephridia of female *M. hirudinaceaus* and the apical sense organ of the same species. Dunagan and Rasheed (1988) described the urogenital system of *Oligacanthorhynchus atratus* (Meyer, 1931) Schmidt 1972 (= *Echinopardalis atrata* Meyer, 1931). Holloway and Gee (1990) described a process in the proboscis of *Corynosoma hamanni* (von Linstow, 1892) Railliet et Henry, 1907, extending from the inner wall of the receptacle, which has been described by Amin in a number of other acanthocephalan species. Marchand and Grita-Timoulaliz (1992) compared the ultrastructure of larval and adult cuticle of *Centrorhynchus milvus* Ward, 1956. Oetinger and Buckner (1993) described the genital vestibule of *Neoechinorhynchus carinatus* Bukner and Buckner, 1993. Foata et al. (2005) described the ultrastructure of spermiogenesis of *M. hirudinaceus*.

Lessons learned from the study of acanthocephalan anatomy

Ultrastructural studies are another way of looking at anatomical structures at a different level of perception. Ultrastructural observations often provide answers to questions of function that gross anatomical questions cannot. For instance, to know the frog by observing its external anatomy is a far cry from knowing the ultrastructure of its muscle cells and nerve insertions that tell us more about how the frog leaps. Similarly, the ultrastructure and the anatomy of nerve cells of the cephalic ganglion or apical organ of acanthocephalans provide a better understanding of the function of connected organs as well as the evolutionary history of higher taxa to which studied specimens are assigned.

Experimental studies

The sub-specialty of experimental parasitology appears to have had reasonable exposure in *JP* despite the presence of other specialty journals that address this need. Van Cleave and Ross (1944) examined the physiological responses of *N. emydis* to various solutions, and Ward (1951) studied the use of antibiotics in artificial media for *in vitro* experiments with Acanthocephala. Kilejan (1963) and Horvath (1971) and Horvath and Fisher (1971) experimented on glycogenesis in *M. moniliformis*. Graff (1964) described the metabolism of ^{14}C-glucose by *M. moniliformis*. Fisher (1964) and McAlister and Fisher (1972) demonstrated the synthesis of trehalose in *M. moniliformis*. Graff (1965) showed the utilization of $^{14}CO_2$ in the production of acid metabolites by *M. moniliformis*. Hibbard and Cable (1968) demonstrated the uptake and metabolism of various chemicals by adult *Paulisentis fractus* Van Cleave and Bangham, 1949. Horvath and Fisher (1971) and Körting and Fairbairn (1972) reported on the enzymes of CO_2 fixation and on anaerobic energy metabolism in *M. moniliformis*, respectively. Uglem and Beck (1972) showed that habitat specificity was correlated with aminopeptidase activity in *Neoechinorhynchus cristatus* Lynch, 1936 (*nec cristatum*) and *N. crassus* Van Cleave, 1919 (*nec crassum*). Starling and Fisher (1975, 1979) described the kinetics and specificity of hexose absorption and carbohydrate transport in *M. moniliformis*. Farland and MacInnis (1978) demonstrated thymidine kinase activity in *M. moniliformis*. Donahue et al. (1981) reported on the carbohydrate regulatory enzymes of *M. hirudinaceus*.

Tokeson and Holmes (1982) studied the effect of temperature and oxygen on the development of *Polymorphus marilis* Van Cleave, 1939, in its amphipod host. Wilkes et al. (1982) studied fumarase activity in *M. moniliformis*. Sangster and Mettrick (1987) showed the effect of cholinergic drugs on muscle contraction in *M. moniliformis*. Richardson and Nickol (2000) experimented with the physiological factors influencing site selection of *L. thecatus* in green sunfish. Reyda and Nickol (2001) compared the biological performances of laboratory raised and wild populations of *M. moniliformis*. Alibert et al. (2002) examined developmental stability in *Gam-marus pulex* Linnaeus, 1758, infected with two species of acanthocephalans. Guinnee and Moore (2004) studied temperature related cockroach fecundity affected by acanthocephalan infections.

Lessons learned from experimental studies on acanthocephalans

Efforts to link physiological and biochemical properties of acanthocephalans with other aspects of host-parasite relationships have been only partially successful. The studies are not always easy to perform, and as is the case with other parasite groups, the focus has been on those acanthocephalan species amenable to laboratory maintenance with *M. moniliformis* being a favorite, likely because its life cycle can be maintained in cockroaches and rats. Species using aquatic hosts such as small crustaceans and fish are sometimes difficult to deal with in the lab, primarily because the intermediate hosts are not always very cooperative in culture. Nevertheless, a rich realm of inquiry into host–parasite relationships awaits a young scientist with the patience and dedication to work with acanthocephalans in the lab.

Surveys, other endeavors, and conclusions

Surveys of parasitic groups, including acanthocepha-lans, did not make the headlines on the pages of *JP* until 1992 (one survey). There were a few others in 1996 (one), 1997 (five), 1998 (two), 2000 (one), 2001 (one), and 2011 (one). Clearly, surveys were not a favored topic to submit, or accept, in *JP*. Several other sub-specialties in acanthocephalan research in *JP* were even less favored over the years, for example, areas such as toxicity, chemistry, development, metabolism, histology, and pathology. Notes on genetic research are selectively incorporated within the molecular taxon-omy section, previously. It is clear that acanthocephalan research and dissemination of knowledge could never be the same without the contributions of authors who have published in *The Journal of Parasitology*.

Literature cited

Alibert, P., L. Bollache, D. Corberant, V. Guesdon, and F. Cézilly. 2002. Parasitic infection and developmental stability: fluctu-ating asymmetry in *Gammarus pulex* infected with two acanthocephalan species. Journal of Parasitology **88**: 47–54.

Allely, Z., J. Moore, and N. J. Gotelli. 1992. *Moniliformis moniliformis* infection has no effect on some behaviors of the cockroach *Diploptera punctata*. Journal of Parasitology **78**: 524–526.

Amin, O. M. 1975. *Acanthocephalus parksidei* sp. n. (Acanthocephala: Echinorhynchidae) from Wisconsin Fishes. Journal of Parasitology **61**: 301–306.

__________. 1982. Acanthocephala. *In* Synopsis and classifica-tion of living organisms, S. P. Parker (ed.). McGraw-Hill Book Co., New York, NY, p. 933–941.

__________. 1985. Classification. *In* Biology of the Acanthocephala, D. W. T. Crompton and B. B. Nickol (eds.). Cambridge University Press, London and New York, p. 27–72.

__________. 1986. Acanthocephala from lake fishes in Wiscon-sin: Host and seasonal distribution of species of the genus *Neoechinorhynchus* Hamann, 1892. Journal of Parasitology **72**: 111–118.

__________. 1987. Key to the families and subfamilies of Acanthocephala, with the erection of a new class (Polyacanthocephala) and a new order (Polyacanthorhynchida). Journal of Parasitology **73**: 1216–1219.

__________. 1987a. Acanthocephala from lake fishes in Wisconsin: Ecology and host relationships of *Pomphorhynchus bulbocolli* (Pomphorhynchidae). Journal of Parasitology **73**: 278–289.

__________. 1987b. Acanthocephala from lake fishes in Wisconsin: Morphometric growth of *Pomphorhynchus bulbocolli* (Pomphorhynchidae). Journal of Parasitology **73**: 806–810.

__________. 1992. Review of the genus *Polymorphus* Lühe, 1911 (Acanthocephala: Polymorphidae) with the synonymization of *Hexaglandula* Petrochenko, 1950, and *Subcorynosoma* Khokhlova, 1967, and a key to the species. Qatar University Science Journal **12**: 115–123.

__________. 2000. Acanthocephala in the Neotropical region. *In* Metazoan parasites in the Neotropics: A systematic and eco-logical approach, G. Salgado-Maldonado, A. N. García Aldrete and V. M. Vidal-Martínez (eds.). Instituto de Biologia, Univer-sidad Nacional Autónomia de México, Mexico City, Mexico, p. 167–174.

__________. 2013. Classification of the Acanthocephala. Folia Parasitologica **60**: 273–305.

__________, and Amin, O. M. 2002. Revision of *Neoechinorhynchus* Stiles & Hassall, 1905 (Acanthocephala: Neoechinorhynchidae) with keys to 88 species in two subgenera. Systematic Parasitology **53**: 1–18.

__________, and N. V. Ha. 2008. On a new acanthocephalan family and a new order, from birds in Vietnam. Journal of Parasitolology **94**: 1305–1310.

__________, R. A. Heckmann, N. A. E. Radwan, J. S. Mantuano Anchundia, and M. A. Zambrano Alcivar. 2009. Redescription of *Rhadinorhynchus ornatus* (Acanthocephala: Rhadinorhynchidae) from skipjack tuna, *Katsuwonus pelamis*, collected in the Pacific Ocean off South America, with special reference to new morphological features. Journal of Parasitology **95**: 656–664.

Ashley, D. C., and B. B. Nickol. 1989. Dynamics of the *Leptorhynchoides thecatus* (Acanthocephala) suprapopulation in a Great Plains reservoir. Journal of Parasitology **75**: 46–54.

Aznar, F. J., G. Pérez-Ponce de Léon, and J. A. Raga. 2006. Sta-tus of *Corynosoma* (Acanthocephala: Polymorphidae) based on anatomical, ecological, and phylogenetic evidence, with the erection of *Pseudocorynosoma*, n. gen. Journal of Parasitology **92**: 548–564.

Balboa, L., A. Hinojosa, C. Riquelme, S. Rodriguez, J. Bustos, and M. George-Nascimento. 2009. Alloxenic distribution of cystacanths of two *Profilicollis* species in sympatric crustacean hosts in Chile. Journal of Parasitology **95**: 1205–1208.

Benesh, D. P., L. M. Duclos, and B. B. Nickol. 2005. The behav-ioral response of amphipods harboring *Corynosoma constrictum* (Acanthocephala) to various components of light. Journal of Parasitology **91**: 731–736.

__________, and E. T. Valtonen. 2007. Effects of *Acanthocephalus lucii (*Acanthocephala) on intermediate host survival and growth: Implications for exploitation strategies. Journal of Parasitology **93**: 735–741.

__________, J. Kitchen, K. Pulkkinen, I. Hakala, and E. T. Valtonen. 2008. The effect of *Echinorhynchus borealis* (Acantho-cephala) infection on the anti-predator behavior of a benthic amphipod. Journal of Parasitology **94**: 542–545.

Bethel, W. M., and J. C. Holmes. 1973. Altered evasive behavior and responses to light in amphipods harboring acanthocephalan cystacanths. Journal of Parasitology **59**: 945–956.

__________, and __________. 1974. Correlation of development of altered evasive behavior in *Gammarus lacustris* (Amphipoda) harboring cystacanths of *Polymorphus paradoxus* (Acanthocephala) with the infectivity to the definitive host. Journal of Parasitology **60**: 272–274.

Bhattacharya, S. B. 2007. Handbook on Indian Acanthocephala. Zoological Survey, Kolkata, India, 255 p.

Bone, L. W. 1974. The chromosomes of *Neoechinorhynchus cylindratus* (Acanthocephala). Journal of Parasitology **60**: 731–732.

Bowen, R. C. 1967. Defense reactions of certain spirobolid millipedes to larval *Macracanthorhynchus ingens*. Journal of Para-sitology **53**: 1092–1095.

Brattey, J. 1988. Life history and population biology of adult *Acanthocephalus lucii* (Acanthocephala: Echinorhynchidae). Journal of Parasitology **74**: 72–80.

Buckner, R. L., and B. B. Nickol. 1979. Geographic and host-related variation among species of *Fessisentis* (Acanthocephala) and confirmation of the *Fessisentis fessus* life cycle. Journal of Parasitology **65**: 161–166.

Budziakowski, M. E., and D. F. Mettrick. 1985. Ultrastructural morphology of the neuropile of the cerebral ganglion of *Moniliformis moniliformis* (Acanthocephala). Journal of Parasitology **71**: 75–85.

Cable, R. M., and W. T. Dill. 1967. The morphology and life history of *Paulisentis fractus* Van Cleave and Bangham, 1949 (Acanthocephala: Neoechinorhynchidae). Journal of Parasitology **53**: 810–817.

Camp, J. W., and H. W. Huizinga. 1979. Altered color, behavior and predation susceptibility of the isopod *Asellus intermedius* infected with *Acanthocephalus dirus*. Journal of Parasitology **65**: 667–669.

__________, and __________. 1980. Seasonal population interactions of *Acanthocephalus dirus* (Van Cleave 1931) in the creek chub, *Semotilus atromaculatus*, and isopod, *Asellus intermedius*. Journal of Parasitology **66**: 299–304.

Carmichael, L. M., and J. Moore 1991. A comparison of behavioral alterations in the brown cockroach *Periplaneta brunnea* and the American cockroach *Periplaneta americana* infected with the acanthocephalan *Moniliformis moniliformis*. Journal of Parasitology **77**: 931–936.

Chervy, L. 2009. Unified terminology for cestode microtriches: a proposal from the International Workshops on Cestode Systematics in 2002–2008. Folia Parasitologica **56**: 199–230.

Cholodkovsky, N. A. 1897. Classification of the Acanthocephala. Trudy San Petersburg. Obshchestva Estestvoispytatelei **28**:14–20.

De Giusti, D. L. 1939. Preliminary note on the life cycle of *Leptorhynchoides thecatus*, an acanthocephalan parasite of fish. Journal of Parasitology **25**: 180.

________. 1949. The life cycle of *Leptorhynchoides thecatus* (Linton), an acanthocephalan of fish. Journal of Parasitology **35**: 437–460.

De Mont, D. J., and K. C. Corkum. 1982. The life cycle of *Octospiniferoides chandleri* Bullock, 1957 (Acantho-cephala: Neoechinorhynchidae) with some observations on parasite-induced, photophilic behavior in ostracods. Journal of Parasitology **68**: 125–130.

Donahue, M. J., N. J. Yacoub, M. R. Kaeini, S. Tu, R. A. Hodzi, and B. G. Harris. 1981. Studies on potential car-bohydrate regulatory enzymes and metabolite levels in *Macracanthorhynchus hirudinaceus*. Journal of Parasitology **67**: 756–758.

Dunagan, T. T., and J. J. Bozzola. 1989. Fine structure of ante-rior terminus of apical sense organ in *Macracanthorhynchus hirudinaceus* (Acanthocephala). Journal of Parasitology **75**: 297–302.

__________, and __________. 1992. Morphology of the apical organ in *Macracanthorhynchus hirudinaceus* (Acanthocephala). Journal of Parasitology **78**: 899–903.

__________, and D. M. Miller. 1976. Nerves originating from the cerebral ganglion of *Moniliformis moniliformis* (Acanthocephala). Journal of Parasitology **62**: 442–450.

__________, and __________. 1978. Anatomy of the genital gan-glion of the male acanthocephalan, *Moniliformis moniliformis*. Journal of Parasitology **64**: 431–435.

__________, and __________. 1981. Anatomy of the cerebral ganglion in *Oligacanthorhynchus tortuosa* (Acanthocephala) from the opossum (*Didelphis virginiana*). Journal of Parasitol-ogy **67**: 881–885.

__________, and __________. 1983. Apical sense organ of *Macra-canthorhynchus hirudinaceus* (Acanthocephala). Journal of Parasitology **69**: 897–902.

__________, and __________. 1985. Microscopic anatomy of the reproductive apparatus of male *Neoechinorhynchus cylindratus* (Acanthocephala). Journal of Parasitology **71**: 329–354.

__________, and __________. 1986. Apical and lateral sense organs in *Moniliformis moniliformis* (Acanthocephala): An SEM view. Journal of Parasitology **72**: 176–178.

__________, and __________. 1987. A model of the cerebral gan-glion in *Macracanthorhynchus hirudinaceus* (Acanthocephala). Journal of Parasitology **73**: 853–855.

__________, and R. M. A. Rashed. 1988. Capsular protonephridia in male *Oligacanthorhynchus atrata* (Acanthocephala). Journal of Parasitology **74**: 180–185.

Dudinák,ˇ V., and V. Šnábel. 2001. Comparative analysis of Slovak and Czech populations of *Pomphorhynchus laevis* (Acanthocephala) using morphological and isoenzyme analysis. Acta Zoologica. Universitatis Comenianae **44**: 41–50.

Elkins, C. A., and B. B. Nickol. 1983. The Epizootiology of *Macra-canthorhynchus ingens* in Louisiana. Journal of Parasitology **69**: 951–956.

Farland, W. H., and A. J. MacInnis. 1978. In vitro thymidine kinase activity: Present in *Hymenolepis diminuta* (Cestoda) and *Moniliformis dubius* (Acanthocephala), but apparently lacking in *Ascaris lumbricoides* (Nematoda). Journal of Parasitology **64**: 564–565.

Foata, J., J.-L. Culioli, and B. Marchand. 2005. Ultrastructure of spermiogenesis and the spermatozoon of *Macracanthorhynchus hirudinaceus* (Pallas, 1781) (Acanthocephala: Archiacantho-cephala), a parasite of the wild boar *Sus scrofa*. Journal of Parasitology **91**: 499–506.

Fontaneto, D., and U. Jondelius. 2011. Broad taxonomic sampling of mitochondrial cytochrome c oxidase subunit 1 does not solve the relationship between Rotifera and Acanthocephala. Zoologischer Anzeiger **250**: 80–85.

Fischthal, J. H. 1950. Additional hosts and geographical distribution records for the common fish acanthocephalan, *Leptorhynchoides thecatus*. Journal of Parasitology **36**: 88.

Fisher, Jr., F. M. 1964. Synthesis of trehalose in Acanthocephala. Journal of Parasitology **50**: 803–804.

Freehling, M., and J. Moore. 1993. Susceptibility of 13 cockroach species to *Moniliformis moniliformis*. Journal of Parasitol-ogy **79**: 442–444.

García-Varela, M., and S. A. Nadler. 2005. Phylogenetic relationships of Palaeacanthocephala (Acanthocephala) inferred from SSU and LSU rRNA gene sequences. Journal of Parasitology **91**: 1401–1409.

__________, and __________. 2006. Phylogenetic relationships among Syndermata inferred from nuclear and mitochondrial gene sequences. Molecular Phylogeny and Evolution **40**: 61–72.

__________, and G. Pérez-Ponce de Léon. 2008. Validating the systematic position of *Profilicollis* Meyer, 1931 and *Hexaglan-dula* Petrochenko, 1950 (Acanthocephala: Polymorphidae) using cytochrome C oxidase (COX 1). Journal of Parasitology **94**: 212–217.

__________, M. P. Cummings, G. Pérez-Ponce de Léon, S. L. Gardner, and J. P. Laclette. 2002. Phylogenetic analysis based on 18S ribosomal RNA gene sequences supports the exis-tence of class Polyacanthocephala (Acanthocephala). Molec-ular Phylogenetics and Evolution **23**: 288–292.

__________, __________, __________, P. de la Torre, M. P. Cummings, S. S. S. Sarma, and J. P. Laclette. 2000. Phyloge-netic relationships of Acanthocephala based on analysis of 18S ribosomal RNA gene sequences. Journal of Molecular Evolution **50**: 532–540.

__________, G. Perez-Ponce de Leon, G. F. J. Aznar, and S. A. Nadler. 2013. Phylogenetic relationship among genera of Polymorphidae (Acanthocephala), inferred from nuclear and mitochondrial gene sequences. Molecular Phylogenetics and Evolution **68**: 176–184.

Garey, J. R., T. J. Near, M. R. Nonnemacher, and S. A. Nadler. 1996. Molecular evidence for Acanthocephala as a subtaxon of Rotifera. Journal of Molecular Evolution **43**: 287–292.

__________, A. Schmidt-Rhaesa, T. J. Near, and S. A. Nadler. 1998. The evolutionary relationships of rotifers and acanthocephalans. Hydrobiologia **387**: 83–89.

Gleason, L. N. 1987. Population dynamics of *Pomphorhynchus bulbocolli* in *Gammarus pseudolimnaeus*. Journal of Parasitology **73**: 1099–1101.

Golvan, Y. J. 1959. Le phylum des Acanthocephala. Deuxième note. La classe de Eoacanthocephala (Van Cleave, 1936). Annales de Parasitologie Humaine et Comparée **34**: 5–52.

__________. 1960. Le phylum des Acanthocephala. Troisième note. La classe des Palaeacanthocephala (Meyer, 1931). Annales de Parasitologie Humaine et Comparée 35: 76–91, 138–165, 350–386, 573–593, 713–723.

__________. 1961. Le phylum des Acanthocephala. Troisième note. La classe des Palaeacanthocephala (Meyer, 1931). Annales de Parasitologie Humaine et Comparée 36: 76–91, 612–647, 717–738.

__________. 1965. Acanthocéphales de Madagascar récoltés par E. R. Brygoo. Annales de Parasitologie Humaine et Comparée **40**: 303–316.

__________. 1969. Systematique des Acanthocephales (Acan-thocephala Rudolphi, 1801), l'ordre des Palaeacanthocephala Meyer, 1931. La superfamille des Echinorhynchidea (Cob-bold, 1876) Golvan et Houin 1963. Mémoires du Muséum National d' Histoire Naturelle, nouvelle ser. A. Zoologie, **57**: 1–373.

__________. 1994. Nomenclature of the Acanthocephala. Research and Reviews in Parasitology **54**: 135–205.

Graff, D. J. 1964. Metabolism of C^{14}-Glucose by *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **50**: 230–234.

__________. 1965. The utilization of C^{14} O_2 in the production of acid metabolites by *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **51**: 72–75.

Guinnee, M. A., and J. Moore. 2004. The effect of para-sitism on host fecundity is dependent on temperature in a cockroach-acanthocephalan system. Journal of Parasitology **90**: 673–377.

Hamann, O. 1892. Das system der Acanthocephalen. Zoologis-cher Anzieger **15**: 195–197.

Harms, C. E. 1965. The life cycle and larval development of *Octospinifer macilentis* (Acanthocephala: Neoechinorhynchidae). Journal of Parasitology **51**: 286–293.

Hibbard, K. M., and R. M. Cable. 1968. The uptake and metabolism of tritiated glucose, tyrosine, and thymidine by adult *Paulisentis fractus* Van Cleave and Bangham, 1949 (Acanthocephala: Neoechinorhynchidae). Journal of Parasitology **54**: 517–523.

Holloway, H. L., and R. J. Gee. 1990. Vesicles in the proboscis of Acanthocephala. Journal of Parasitology **76**: 585–587.

Hopp, W. B. 1954. Studies on the morphology and life cycle of *Neoechinorhynchus emydis* (Leidy), an acanthocephalan para-site of the map turtle, *Graptemys geographica* (Le Sueur). Jour-nal of Parasitology **40**: 284–299.

Horvath, K. 1971. Glycogen metabolism in larval *Monili-formis dubius* (Acanthocephala). Journal of Parasitology **57**: 132–136.

__________, and F. M. Fisher, Jr. 1971. Enzymes of CO_2 fixation in larval and adult *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **57**: 440–442.

Hutton, T. L., and D. F. Oetinger 1980. Morphogenesis of the proboscis hooks of an archiacanthocephalan, *Moniliformis moniliformis* (Bremser 1811) Travassos 1915. Journal of Parasitology **66**: 965–972.

Jilek, R. 1978. Seasonal occurrence and host specificity of *Gracilisentis gracilisentis* and *Tanaorhamphus longirostris* (Acan-thocephala: Neoechinorhynchidae) in Crab Orchard Lake, Illinois. Journal of Parasitology **64**: 951–952.

Jones, A. W., and H. L. Ward 1950. The chromosomes of *Macra-canthorhynchus hirudinaceus* (Pallas). Journal of Parasitology **36**: 86.

Khatoon, N., and F. M. Bilqees. 2011. Acanthocephala of vertebrates. A world record. Dr. Müller GmbH and Co., VDM Verlag, Saarbrücken, Germany, 566 p.

Kilejan, A. 1963. The effect of carbon dioxide on glycogenesis in *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **49**: 862–863.

Kopp, D. A., D. A. Elke, S. C. Caddigan, A. Raj, L. Rodriguez, M. K. Young, and T. C. Sparkes. 2011. Dispersal in the acan-thocephalan *Acanthocephalus dirus*. Journal of Parasitology **97**: 1101–1105.

Körting, W., and D. Fairbairn. 1972. Anaerobic energy metabolism in *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **58**: 45–50.

Krapf, K., and T. T. Dunagan 1987. Structural features of the protonephridia in female *Macracanthorhynchus hirudinaceus* (Acanthocephala). Journal of Parasitology **73**: 1176–1181.

Kristensen, R. M. 2002. An introduction to Loricifera, Cycliophora, and Micrognathozoa. Integrative and Comparative Biology **42**: 641–652

Leuckart, R. 1848. Über die Morphologie und Verwandtschaftsverhältnisse der wirbellosen Thiere. Ein Beitrag zur Charakteristik und Classification der Thierischen Formen. F. Vieweg und Sohn, Braunschweig, Germany, 180 p.

Lühe, M. 1904–1905. Geschichte und Ergebnisse der Echinorhynchen-Forschung bis auf Westrumb (1821) (Mit Bemerkungen über alte und nueu Gattungen der Acanthocephalen). Zoologische Annalen, Zeitschrift Geschichte Zoologie Herausgegeben von B. Braun. Würsburg, Germany, **1**: 139–353.

Marchand, B. 1984. A comparative ultrastructural study of the shell surrounding the mature acanthor larvae of 13 acanthocephalan species. Journal of Parasitology **70**: 886–901.

__________, and Grita-Timoulaliz. 1992. Comparative ultrastructural study of the cuticle of larvae and adults of *Centorhynchus milvus* Ward 1956, (Acanthocephala, Centrorhynchidae). Journal of Parasitology **78**: 355–359.

Martinez-Aquino, A., M. E. Reyna-Fabián, Z. R. Rosas-Valde, U. Razo-Mendivil, G. Pérez-Ponce de León, and M. García-Valera. 2009. Detecting a complex of cryptic species within *Neoechinorhynchus golvani* (Acanthocephala: Neoechinorhynchidae) inferred from ITSs and LSU rDNA gene sequences. Journal of Parasitology **95**: 1040–1047.

Maynard, B. J., T. A. Wellnitz, N. Zanini, W. G. Wright, and B. S. Dezfull. 1998. Parasite-altered behavior in a crustacean intermediate host: Field and laboratory studies. Journal of Parasitology **84**: 1102–1106.

McAlister, R. O., and F. M. Fisher, Jr. 1972. The biosynthesis of trehalose in *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **58**: 51–62.

McLennan, D. A., and V. L. Shires. 1995. Correlation between the level of infection with *Bunodera inconstans* and *Neoechinorhynchus rutili* and behavioral intensity in female brook sticklebacks. Journal of Parasitology **81**: 675–682.

Merriott, S. V., and I. Pratt. 1964. The life history of *Neoechinorhynchus rutili* and its development in the intermediate host (Acanthocephala: Neoechinorhynchidae). Journal of Parasitology **50**: 394–400.

Meyer, A. 1931. Neue Acanthocephalen aus dem Berliner Museum. Burgründung eines neue Acanthocephalen Systems auf Grund einer Untersuchung der Berliner Sammlung. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie Geographie Tiere **62**: 53–108.

__________. 1932. Acanthocephala. *In* Dr. H.G. Bronn's Klassen und Ordnungen des Tier-Reichs. Akademische Verlagsgesellschaft MBH, Leipzig, Germany **4**: 1–332.

__________. 1933. Acanthocephala. *In* Dr. H.G. Bronn's Klassen und Ordnungen des Tier-Reichs. Akademische Verlagsgesellschaft MBH, Leipzig, Germany **4**: 333–582.

Miller, D. M., and T. T. Dunagan. 1978. Organization of the lacunar system in the acanthocephalan, *Oligacanthorhynchus tortuosa*. Journal of Parasitology **64**: 436–439.

___________, and __________. 1983. A support cell to the apical and lateral sensory organs in *Macracanthorhynchus hirudinaceus* (Acanthocephala). Journal of Parasitology **69**: 534–538.

Min, G. S., and J. K. Park. 2009. Eurotatorian paraphyly: Revis-itingphylogenetic relationships based on the complete mito-chondrial genome sequence of *Rotaria rotatoria* (Bdelloidea: Rotifera: Syndermata). BMC Genomics **10**: 533.

Monks, S. 2001. Phylogeny of the Acanthocephala based on morphological characters. Systematic Parasitology **48**: 81–116.

__________, G. Pulido-Flores, and J. Violante-González. 2011. A new species of *Neoechinorhynchus* (Acanthocephala: Neoechinorhynchidae) in *Dormitator latifrons* (Perciformes: Eleotridae) from the Pacific coast of Mexico. Comparative Parasitology. **78**: 21–28.

Moore, D. V. 1946. Studies on the life history and development of *Macracanthorhynchus ingens* Meyer, 1933, with a redescrip-tion of the adult worm. Journal of Parasitology **32**: 387–399.

__________. 1962. Morphology, life history, and development of the acanthocephalan *Mediorhynchus grandis* Van Cleave, 1916. Journal of Parasitology **48**: 76–86.

Moore, J. 1983. Altered behavior in cockroaches (*Periplan-eta americana*) infected with an archiacanthocephalan, *Moniliformis moniliformis*. Journal of Parasitology **69**: 1174–1176.

__________, and N. J. Gottelli. 1992. *Moniliformis moniliformis* increases cryptic behaviors in the cockroach *Supella longipalpa*. Journal of Parasitology **78**: 49–53.

________, and ________. 1996. Evolutionary patterns of altered behavior and susceptibility in parasitized hosts. Evolution **50**: 807–819.

__________, M. Freehling, and N. J. Gottelli. 1994. Altered behavior in two species of blattid cockroaches infected with *Moniliformis moniliformis* (Acanthocephala). Journal of Parasitology **80**: 220–223.

Moser, M., and J. Hsieh. 1992. Biological tags for stock separation in Pacific herring *Clupea harengus pallasi* in California. Journal of Parasitology **78**: 54–60.

Muzzall, P. M. 1980. Ecology and seasonal abundance of three acanthocephalan species infecting white suckers in SE New Hampshire. Journal of Parasitology **66**: 127–133.

__________, and W. L. Bullock. 1978. Seasonal occurrence and host-parasite relationships of *Neoechinorhynchus saginatus* Van Cleave and Bangham 1949 in the fallfish, *Semotilus corporalis* (Mitchill). Journal of Parasitology **64**: 860–865.

Near, T. J. 2002. Acanthocephalan phylogeny and the evolution of parasitism. Integrative and Comparative Biology **42**: 668–677.

__________, J. R. Garey, and S. A. Nadler. 1998. Phylogenetic relationships of the Acanthocephala inferred from 18S ribo-somal DNA sequences. Molecular Phylogenetics and Evolu-tion **10**: 287–298.

Nickol, B. B. 1977. Life history and host specificity of *Mediorhynchus centurorum* Nickol 1969 (Acanthocephala: Gigantorhynchidae). Journal of Parasitology **63**: 104–111.

__________, D. W. T. Crompton, and D. W. Searle. 1999. Rein-troduction of *Profilicollis* Meyer, 1931, as a genus in Acan-thocephala: Significance of the intermediate host. Journal of Parasitology **85**: 716–718.

Oetinger, D. F., and R. L. Buckner. 1993. Morphology of the genital vestibule of *Neoechinorhynchus carinatus* (Acanthocephala: Neoechinorhynchidae). Journal of Parasitology **79**: 930–934.

__________, and B. B. Nickol. 1982. Spectrophotometric characterization of integumental pigments from uninfected and *Acanthocephalus dirus*-infected *Asellus intermedius*. Journal of Parasitology **68**: 270–275.

__________, and __________. 1982. Developmental relationships between acanthocephalans and altered pigmentation in freshwater isopods. Journal of Parasitology **68**: 463–469.

Olson, P. D., and B. B. Nickol. 1996. Comparison of *Leptorhyn-choides thecatus* (Acanthocephala) recruitment into green sun-fish and largemouth bass populations. Journal of Parasitology **82**: 702–706.

Olson, R. E., and I. Pratt 1971. The life cycle and larval development of *Echinorhynchus lageniformis* Ekbaum, 1938 (Acan-thocephala: Echinorhynchidae). Journal of Parasitology **57**: 143–149.

Perrot-Minnot, M.-J. 2004. Larval morphology, genetic divergence, and contrasting levels of host manipulation between forms of *Pomphorhynchus laevis* (Acanthocephala). International Journal for Parasitology **34**: 45–54.

Petrochenko, V. I. 1952. On the position of the Acanthocephala in the zoological system. (Phylogenetic connections of the Acanthocephala with other groups of invertebrates). Zoologicheskii Zhurnal **31**: 288–327.

__________. 1956. Acanthocephala of domestic and wild Animals. Vol. **1**. Izdatel'stvo Akademii Nauk SSSR. English translation by Israel Program for Scientific Translations, Ltd., Jerusalem, Israel (1971), 465 p.

Podesta, R. B., and J. C. Holmes. 1970. The life cycles of three polymorphids (Acanthocephala) occurring as juveniles in *Hyalella azteca* (Amphipoda) at Cooking Lake, Alberta. Journal of Parasitology **56**: 1118–1123.

Rauque, C. A., L. G. Semenas, and G. P. Viozzi. 2006. Seasonality of recruitment and reproduction of *Acanthocephalus tumescens* (Acanthocephala) in fishes from Lake Moreno (Patagonia, Argentina). Journal of Parasitology **92**: 1265–1269.

__________, and L. Semenas. 2011. Parasite volume as an indicator of competition: The case of *Acanthocephalus tumescens* and *Pseudocorynosoma* sp. (Acanthocephala) in their intermediate host. Journal of Parasitology **97**: 999–1002.

Reish, D. J. 1950. Preliminary note on the life cycle of the acan-thocephalan, *Polymorphus kenti* Van Cleave, 1947. Journal of Parasitology **36**: 496.

Reyda, F. B., and B. B. Nickol. 2001. A comparison of biologi-cal performances among a laboratory-isolated population and two wild populations of *Moniliformis moniliformis*. Journal of Parasitology **87**: 330–338.

Richardson, D. J., and B. B. Nickol. 1995. The genus *Centrorhynchus* (Acanthocephala) in North America with description of *Centrorhynchus robustus* n. sp., redescription of *Centrorhynchus conspectus*, and a key to species. Journal of Parasitology **81**: 767–772.

__________, and __________. 2000. Experimental investigation of physiological factors that may influence microhabitat specificity exhibited by *Leptorhynchoides thecatus* (Acantho-cephala) in green sunfish (*Lepomis cyanellus*). Journal of Parasitology **86**: 685–690.

Rieger, R. M., and S. Tyler. 1995. Sister-group relationship of Gnathostomulida and Rotifera – Acanthocephala. Invertebrate Biology **114**: 186–188.

Robinson, E. S. 1964. Chromosome morphology and behavior in *Macracanthorhynchus hirudinaceus*. Journal of Parasitology **50**: 694–697.

__________. 1965. The chromosomes of *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **51**: 430–432.

__________. 1973. Growth and differentiation of giant nuclei in *Moniliformis* (Acanthocephala). Journal of Parasitology **59**: 678–684.

Rosas-Valdez, R., J. J. Morrone, and M. García-Varela. 2012. Molecular phylogenetics of *Floridosentis* Ward, 1953 (Acanthocephala: Neoechinorhynchidae) parasites of mullets (Osteichthyes) from Mexico, using 28S rDNA sequences. Journal of Parasitology **98**: 855–862.

Rudolphi, C. A. 1802. Fortsetzung der Beobachtungen uber die Eingeweidwurmer. Wiedmann's Archiv Zoologie Braunschweig **2**: 1–67.

Salgado-Maldonado, G. 2006. Checklist of helminth parasites of freshwater fishes from Mexico. Zootaxa **1324**: 1–357.

__________, and O. M. Amin. 2009. Acanthocephala of the Gulf of Mexico. *In* Origin, waters, and biota. Vol. **1**, Biodiversity, D. L. Felder and D.K. Camp (eds.). Texas University Press, Corpus Christi, Texas, p. 539–552.

Samuel, G., and W. L. Bullock. 1981. Life cycle of *Paratenuisen-tis ambiguus* (Van Cleave, 1921) Bullock and Samuel, 1975 (Acanthocephala: Tenuisentidae). Journal of Parasitology **67**: 214–217.

Sangster, N. C., and D. F. Mettrick. 1987. Effects of cholinergic drugs on muscle contraction in *Moniliformis moniliformis* (Acanthocephala). Journal of Parasitology **73**: 998–1004.

Schmidt, G. D. 1972. Revision of class Archiacanthocephala Meyer, 1931 (Phylum Acanthocephala), with emphasis on Oligacanthorhynchidae Southwell and MacFie, 1925. Journal of Parasitology **58**: 290–297.

__________. 1977. Praesomal musculature of the acanthocephalan genus *Mediorhynchus*. Journal of Parasitology **63**: 112–116.

__________, and E. J. Hugghins. 1973a. Acanthocephala of South American fishes. Part 1. Eoacanthocephala. Journal of Parasitology **59**: 829–835.

__________, and __________. 1973b. Acanthocephala of South American fishes. Part 2. Palaeacanthocephala. Journal of Parasitology **59**: 836–838.

__________, and K. A. Neiland. 1966. Helminth fauna of Nicaragua. III. Some Acanthocephala of birds, including three new species of *Centrorhynchus*. Journal of Parasitology **52**: 739–745.

__________, and R. E. Kuntz. 1967*a*. Notes on the life cycle of *Polymorphus (Profilicollis) formosus* sp. n., and records of *Arhythmorhynchus hispidus* Van Cleave, 1925 (Acanthocephala) from Taiwan. Journal of Parasitology **53**: 805–809.

__________, and __________. 1967b. Revision of Porrorchinae (Acanthocephala: Plagiorhynchidae) with descriptions of two new genera and three new species. Journal of Parasitology **53**: 130–141.

__________, and O. W. Olsen. 1964. Life cycle and development of *Prosthorhynchus formosus* (Van Cleave, 1918) Travassos, 1926, an acanthocephalan parasite of birds. Journal of Parasitology **50**: 721–730.

Seidenberg, A. J. 1973. Ecology of the acanthocephalan, *Acanthocephalus dirus* (Van Cleave, 1931), in its intermediate host, *Asellus intermedius* Forbes (Crustacea: Isopoda). Journal of Parasitology **59**: 957–962.

Skrjabin, K. I., and R. E. S. Shults. 1931. Helminthoses of man (Foundations of Medical Helminthology) for medical doctors and veterinarians, biologists and students. Part II. State Med-ical Publisher, Moscow, Russia, 250 p.

Smales, L. R. 2002. Species of *Mediorhynchus* (Acanthocephala: Gigantorhynchidae) in Australian birds with the description of *Mediorhynchus colluricinclae* n. sp. Journal of Parasitology **88**: 375–381.

Sobecka, E., B. Szostakowska, K. Mackenzie, W. Hemmingsen, S. Prajsnar, and M. Eydal. 2012. Genetic and morphological variation in *Echinorhynchus gadi* Zoega in Müller, 1776 (Acanthocephala: Echinorhynchidae) from Atlantic cod *Gadus morhua* L. Journal of Helminthololgy **86**: 16–25.

Southwell, T., and J. W. S. MacFie. 1925. On a collection of Acanthocephala in the Liverpool School of Tropical Medicine. Annals of Tropical Medicine and Parasitology **19**: 141–184.

ŠpakulováM. M. Perrot-Minnot, and B. Neuhaus. 2011 Resurrection of *Pomphorhynchus tereticollis* (Rudolphi, 1809) (Acanthocephala: Pomphorhynchidae) based on new morphological and molecular data. Helminthologia **48**: 268–277.

Starling, J. A., and F. M. Fisher, Jr. 1975. Carbohydrate transport in *Moniliformis dubius* (Acanthocephala). I. The kinetics and specificity of hexose absorption. Journal of Parasitology **61**: 977–990.

__________, and __________. 1979. Carbohydrate transport in *Moniliformis dubius* (Acanthocephala). III. Post-absorptive fate of fructose, mannose, and galactose. Journal of Parasitology **65**: 8–13.

Steinauer, M. L., B. B. Nickol, R. Broughton, and G. Orti. 2005. First sequenced mitochondrial genome from the phylum Acanthocephala (*Leptorhynchoides thecatus*) and its phylogenetic position within Metazoa. Journal of Molecular Evolution **60**: 706–715.

Stoddart, R. C. 1965. New intermediate hosts in the life cycle of *Prosthenorchis elegans* (Diesing, 1851), an acanthocephalan parasite of primates. Journal of Parasitology **51**: 645–649.

________, D. W. T. Crompton, and D. E. Walters. 1991. Influence of host strain and helminth isolate on the first phase of the relationship between rats and *Moniliformis moniliformis* (Acanthocephala). Journal of Parasitology **77**: 372–377.

Stunkard, H. W. 1965. New intermediate host in the life cycle of *Prosthenorchis elegans* (Diesing, 1851), an acanthocephalan parasite of primates. Journal of Parasitology **51**: 645–649.

Thapar, G. S. 1927. On *Acanthogyrus* n. gen. from the intestine of the Indian fish *Labeo rohita*, with a note on the classification of the Acanthocephala. Journal of Helminthology **5**: 109.

Tkach, V. V., O. I. Lisitsyna, J. L. Crossley, T. T. Binh, and S. F. Bush. 2013. Morphological and molecular differentiation of two new species of *Pseudoacanthocephalus* Petrochenko, 1958 (Acanthocephala: Echinorhynchidae) from amphibians and reptiles in the Philippines, with identification key for the genus. Systematic Parasitology **85**: 11–26.

Tokeson, J. P. E., and J. C. Holmes 1982. The effects of temperature and oxygen on the development of *Polymorphus marilis* (Acanthocephala) in *Gammarus lacustris* (Amphipoda). Jour-nal of Parasitology **68**: 112–119.

Travassos, L. 1926. Contribuições para o conhecimento da fauna helminthologica brasileira. XX. Revisaeo dos acanthocefalos brasileiros. Part II. Fam. Echinorhynchidae. Subfam. Centrorhynchinae Travassos, 1919. Memorias do Instituto Oswaldo Cruz **19**: 31–125.

Trejo, A. 1992. A comparative study of the host-parasite relationship of *Pomphorhynchus patagonicus* (Acanthocephala) in two species of fish from Lake Rosario (Chubut, Argentina). Journal of Parasitology **78**: 711–715.

Uglem, G. L. 1972. The life cycle of *Neoechinorhynchus cristatus* Lynch, 1936 (Acanthocephala) with notes on the hatching of eggs. Journal of Parasitology **58**: 1071–1074.

__________, and S. M. Beck. 1972. Habitat specificity and correlated aminopeptidase activity in the acanthocepha-lans *Neoechinorhynchus cristatus* and *N. crassus*. Journal of Parasitology **58**: 911–920.

__________, and O. R. Larson. 1969. The life history and larval development of *Neoechinorhynchus saginatus* Van Cleave and Bangham, 1949 (Acanthocephala: Neoechinorhynchidae). Journal of Parasitology **55**: 1212–1217.

Väinölä, R., E. T. Valtonen, and D. I. Gibson. 1994. Molecu-lar systematic in the acanthocephalan genus *Echinorhynchus* (sensu lato) in northern Europe. Parasitology **108**: 105–114.

Van Cleave, H. J. 1914. *Eorhynchus*: a proposed new name for *Neorhynchus* Hamann Preoccupied. Journal of Parasitology **1**: 50–51.

__________. 1936. The recognition of a new order in the Acan-thocephala. Journal of Parasitology **22**: 202–206.

__________. 1941. Relationships of the Acanthocephala. American Naturalist **75**: 31–47.

__________. 1947. The Eoacanthocephala of North Amer-ica, including the description of *Eocollis arcanus*, new genus and new species, superficially resembling the genus *Pomphorhynchus*. Journal of Parasitology **33**: 285–296.

__________. 1948: Expanding horizons in the recognition of a phylum. Journal of Parasitology **34**: 1–20.

__________. 1949: Morphological and phylogenetic interpretation of cement glands in the Acanthocephala. Journal of Mor-phology **84**: 427–457.

__________. 1951. Speciation and formation of genera in the Acanthocephala. Anatomical Record **111**: 525–526.

__________. 1952. Acanthocephalan nomenclature introduced by Lauro Travassos. Proceedings of the Helminthological Soci-ety of Washington **19**: 1–8.

__________, H. J., and E. L. Ross. 1944. Physiological responses of *Neoechinorhynchus emydis* (Acanthocephala) to various solu-tions. Journal of Parasitology **30**: 369–372.

Verweyen, L., L. S. Klimpe, and H. W. Palm. 2011. Molecular phylogeny of the Acanthocephala (class Palaeacanthocephala) with a paraphyletic assemblage of the orders Polymorphida and Echinorhynchida. PLoS ONE **6**: e28285.

Wahl, G. M., and T. C. Sparkes. 2012. Egg dispersal in the acan-thocephalan *Acanthocephalus dims*: Field data. Journal of Par-asitology **98**: 894–896.

Walkey, M. 1967. The ecology of *Neoechinorhynchus rutili* (Müller). Journal of Parasitology **53**: 795–804.

Ward, H. L. 1951. The use of antibiotics in artificial media for *in vitro* experiments with Acanthocephala. Journal of Parasitology **37**: 319.

Weber, M., A. R. Wey-Fabrizius, L. P. Lowski, A. Witek, R. O. Schill, R. L. Suga, H. Herlyn, and T. Hankeln. 2013. Phylogenetic analyses of endoparasitic Acanthocephala based on mitochondrial genomes suggest secondary loss of sensory organs. Molecular Phylogenetics and Evolution **66**: 182–189.

Welch, D. B. M. 2000. Evidence from a protein-coding gene that acanthocephalans are rotifers. Invertebrate Biology **119**: 17–26.

West, A. J. 1964. The acanthor membranes of two species of Acanthocephala. Journal of Parasitology **50**: 731–734.

Wilkes, J., R. A. Cornish, and D. F. Mettrick. 1982. Fumarase activity in *Moniliformis dubius* (Acanthocephala). Journal of Parasitology **68**: 162–163.

Witek, A., H. Herlyn, I. Ebersberger, D. B. M. Welch, and T. Hankeln. 2009. Support for the monophyletic origin of Gnathifera from phylogenomics. Molecular Phylogenetics and Evolution **53**: 1037–1041.

__________, __________, A. Meyer, L. Boell, G. Bucher, and T. Hankeln. 2008. EST based phylogenomics of Syndermata questions monophyly of Eurotatoria. BMC Evolutionary Biology **8**: 345.

Witenberg, G. 1932a. Akanthocephalen Studien. I. Uber einige für Systematik der Akanthocephalen wichtige anatomisch Merkmale. Bolletino di Zoologia, Publicato della Unione Zoologica Italiana **3**: 243–252.

Witenberg, G. 1932b. Akanthocephalen Studien. II. Über das System der Acanthocephalen. Bolletino di Zoologia, Publicato della Unione Zoologica Italiana **3**: 253–256.

Wright, R. D., and R. D. Lumsden. 1968. Ultrastructural and histochemical properties of the acanthocephalan epicuticle. Journal of Parasitology **54**: 1111–1123.

__________, and __________. 1969. Ultrastructure of the tegu-mentary pore-canal system of the acanthocephalan *Monili-formis dubius*. Journal of Parasitology **55**: 993–1003.

Yamaguti, S. 1963. Acanthocephala. Systema helminthum. John Wiley & Sons, Ltd, London, U.K., 423 p.

Zhao, B., and M. X. Wang. 1992. Ultrastructural study of the defense reaction against the larvae of *Macracanthorhynchus hirudinaceus* in laboratory-infected beetles. Journal of Parasitology **78**: 1098–1101.

Zrzavy,´ J. 2001. The interrelationships of metazoan parasites: a review of phylum- and higher- level hypotheses from recent morphological and molecular phylogenetic analyses. Folia Parasitologica **48**: 81–103.