Host relationships and geographic distribution of species of *Acanthobothrium* Blanchard, 1848 (Onchoproteocephalidea, Onchobothriidae) in elasmobranchs: a metadata analysis

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Abstract

Species of *Acanthobothrium* have been documented as parasites of the spiral intestine of elasmobranchs. Results of a metadata analysis indicate that 114 species of elasmobranchs have been reported as hosts of 200 species of *Acanthobothrium*. The metadata analysis revealed that 3.7% of species of sharks and 14.9% of species of rays that have been reported as hosts to date; some species are parasitized by more than one species of *Acanthobothrium*. This work provides a Category designation, as proposed by Ghoshroy and Caira (2001), for each species of *Acanthobothrium*. These Category designations are a tool to facilitate comparisons among members of *Acanthobothrium* for descriptions of new species in the future.

Keywords

Biodiversity, Elasmobranchii, Eucestoda, geographic distribution, rays, sharks
Introduction

According to Last et al. (2016b), there are 34 families comprised of 516 valid species of sharks and 26 families that include 633 valid species of rays. Since that publication, six new species of sharks and rays were described by: Yokota and Carvalho (2017) (two species of rays), Vaz and Carvalho (2018) (one species of shark), Rutledge (2019) (one species of ray), Grace et al. (2019) (one species of shark) and Concha et al. (2019) (one species of ray). This brought the current number of recognized species to 517 species of sharks and 637 species of rays.

Elasmobranchs (sharks, skates and rays) are host to a great variety of parasites in nature, particularly helminths. Acanthobothrium Blanchard, 1848 (Onchoproteocephalidea) is the most diverse genus that has been reported as parasite of the spiral intestine of elasmobranchs (Caira and Jensen 2017). At the present time, 201 species of Acanthobothrium are considered to be valid (Maleki et al. 2013; Caira and Jensen 2017; Rodriguez-Ibarra et al. 2018; Franzese and Ivanov 2018; Maleki et al. 2019; Zaragoza-Tapia et al. 2019, 2020). The genus consists of species that exclusively parasitize elasmobranchs as adults and, in many cases, individual species are thought to parasitize only a single species of elasmobranch (Caira 2011; Caira and Jensen 2017). Therefore, the genus Acanthobothrium is an excellent model for future studies of host-parasite co-speciation.

The main goal of this work is to provide a revised checklist based on a metadata analysis of the host relationships of members of Acanthobothrium and their geographic distribution based on records that have been generated from different parts of the world. The checklist focuses on the 201 valid species of Acanthobothrium and reports correlated with the genera and species of elasmobranchs, and includes the geographical distribution of each.

The number of species of Acanthobothrium continues to grow and there are still regions of the world without a single report of this genus (see Figure 1). For some time, the process of distinguishing new species of Acanthobothrium from existing species has become more and more unwieldy because of the large number of species. As an identification tool, Ghoshroy and Caira (2001) developed a categorical method for identifying species for initial comparisons. Therefore, in order to provide an update to this method, categorical designations are provided in the present checklist for each species of Acanthobothrium in the manner proposed by Ghoshroy and Caira (2001). The categories are based on and obtained from the combination of four quantitative characters: total length of the worm; the number of proglottids comprising the strobila; the number of testes per proglottid; and symmetry of the ovarian lobes. This categorical designation allows parasitologists working with this genus to postulate a group of similar species, those of the same category designation, for comparison of a new species or to aid in the preliminary identification of known species. As an additional aid, in the checklist the accession number, if known, of type specimens of each species is provided.
Materials and methods

The checklist, updated until March 2020, was based on bibliographical information from two sources of information: 1. a compilation of the records of species of *Acanthobothrium* as originally described, complemented by information gathered from Global Cestode Database (Caira et al. 2019) and from recent compilation studies (e.g., Ghoshroy and Caira 2001; Campbell and Beveridge 2002; Fyler and Caira 2006; Caira and Jensen 2017); and 2. information for the distribution and taxonomy of elasmobranchs that integrated a bibliographical search using different databases of literature published to date (e.g., Del Moral-Flores et al. 2015; Last et al. 2016b; Merlo-Serna and García-Prieto 2016; Alves et al. 2017) and data from FishBase (Froese and Pauly 2019).

In the checklist, the species of *Acanthobothrium* are arranged in alphabetical order. The scientific names and geographic distribution of elasmobranchs have been updated based on Last et al. (2016a, 2016b), Amaral et al. (2018) and Froese and Pauly (2019). The regional classification scheme of the geographic distribution of the hosts is according to Last et al. (2016b) with additional information from Froese and Pauly (2019). The following abbreviations are used for biogeographic regions (see Figure 1):

| Abbreviation | Region                  |
|--------------|-------------------------|
| ARC          | Arctic Ocean            |
| ECA          | Eastern Central Atlantic|
| ECP          | Eastern Central Pacific  |
| EIO          | Eastern Indian Ocean     |
| ENA          | Eastern North Atlantic   |
| ENP          | Eastern North Pacific    |
| ESA          | Eastern South Atlantic   |
| ESP          | Eastern South Pacific    |
| MED          | Mediterranean Sea        |
| NIO          | Northern Indian Ocean    |
| SOC          | Southern (Antarctic) Ocean |
| WCA          | Western Central Atlantic|
| WCP          | Western Central Pacific  |
| WIO          | Western Indian Ocean     |
| WNA          | Western North Atlantic   |
| WNP          | Western North Pacific    |
| WSA          | Western South Atlantic   |
| WSP          | Western South Pacific    |

Information for each species of *Acanthobothrium* presented herein includes the name of the species, authority (original description referenced in the literature cited), abbreviation of the name of the collection where specimens are deposited and the accession numbers of the specimens, followed by the status of the specimens (holotype, paratype, neotype, syntype or voucher). The acronym “NR” was used for data that are not reported in the original source. Localities (type or/and additional localities) were given and referenced in the literature cited. A Category designation was supplied for all species using the categorical method proposed by Ghoshroy and Caira (2001).

The categorical method was developed as a system of grouping species of *Acanthobothrium* based on the combination of four qualitative characters: the total length of worms- ≤ 15 mm = S (short) or > 15 mm = L (long); the number of proglottids comprising the strobila- ≤ 50 = F (few) or > 50 = M (many); the number of testes per proglottid- ≤ 80 = F (few) or > 80 = M (many); and symmetry of the ovarian lobes-symmetrical = S or asymmetrical = A. Of the possible combinations the following 10...
Figure 1. Type localities of species of *Acanthobothrium* reported worldwide and the biogeographic regions (Last et al. 2016b) of the geographic distribution of their hosts (see Table 1).

categories currently are recognized and coded as follows: 1 = SFFS; 2 = SFFA; 3 = LMMA; 4 = LMMS; 5 = LMFS; 6 = LMFA; 7 = LFFA; 8 = SMFS; 9 = LFFS; 10 = SMMS. This method limited the number of necessary comparisons required in the description between known species with new species assigned to the same Category. For this work, the categories and characteristics were used as in Ghoshroy and Caira (2001) and Fyler and Caira (2006) but the character values are as given in the original descriptions or as supplemented by the most recent taxonomic publications. In the Category designation, the type species is identified by number for this classification; the symbol “–” was used for the additional reports of species with additional hosts and/or localities.

For specimens deposited in a formal collection, acronyms are as follows:

**AMS** Australian Museum, Sydney;

**CH-MHNJP** Colecciones Helmintológicas del Museo de Historia Natural “Javier Prado” y del Instituto de Medicina Tropical “Daniel. A. Carrión”, Universidad Mayor de San Marcos, Perú;

**CHE** Colección de Helminos, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Pachuca, México;

**CHIOC** Coleção Helmintológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil;

**CNHE** Colección Nacional de Helminos del Instituto de Biología, Universidad Nacional Autónoma de México, México;
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DMNZ  
Dominion Museum (=National Museum), New Zealand;

DZAUW  
Department of Zoology, Andhra University, Waltair, India;

DZCJ  
Department of Zoology, Bipin Bihari, P. G. College, Jhansi, India;

HWML  
University of Nebraska State Museum, Harold W. Manter Laboratory, Division of Parasitology, Lincoln, Nebraska, United States;

IPCAS  
Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic;

IPMB  
Institut Penyelidikan Marin Borneo (Borneo Marine Research Institute), Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia;

LRP  
Lawrence R. Penner Parasitology Collection, Helminthological Collection, University of Connecticut, Storrs, Connecticut, United States;

MACN-Pa  
Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina;

MEPN  
Museum of the Escuela Politecnica Nacional, Quito, Ecuador;

MHNLS  
Museo de Historia Natural La Salle, Caracas, Venezuela;

MHNP  
Museo de Historia Natural, Lima, Peru;

MLP  
Museo de Ciencias Naturales de La Plata, Departamento de Zoología Invertebrados (Parasitología), Argentina;

MNHG  
Museum of Natural History, Geneva, Switzerland;

MNHN  
Muséum National d’Histoire Naturelle, Paris;

MNHNC  
Museo Nacional de Historia Natural de Chile;

MPM  
Meguro Parasitology Museum, Tokyo, Japan;

MZUM (P)  
Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia;

MZUSP  
Museu de Zoologia da Universidade de São Paulo, Brazil;

NMUK  
The Natural History Museum, London;

NMNS  
National Museum of Natural Science, Taichung, Taiwan;

PRLXU  
Parasitology Research Laboratory, Xiamen University, China;

QM  
Queensland Museum, Brisbane, Queensland, Australia;

SAM AHC  
South Australian Museum, Adelaide, Australia;

SBC  
Sarawak Biodiversity Center, Kuching, Sarawak, Malaysia;

SPUK  
School of Parasitology, Department of Zoology, University of Karachi, Pakistan;

SYSU  
School of Life Sciences, Sun Yat-sen University;

UAA  
Department of Zoology, University of Allahabad, Allahabad, India;

USNPC  
United States National Parasite Collection, Beltsville, Maryland, United States;

ZCUOK  
Zoological Collection, University of Kurdistan, Sanandaj, Iran;

ZIMC  
Collection of the Zoological Survey of India, Indian Museum, Calcutta and the Collection of the Department of Zoology, the University of Allahabad, India;

ZMB  
Natural History Museum Berlin, Germany;

ZUTC  
Collection of the Zoological Museum, University of Tehran, Tehran, Iran.
| Species of Acanthobothrium reported from the different species of elasmobranchs of the world. Abbreviations: Cd = Geographical distribution; Ht = Holo-type; Nr = Neotype; Pr = Paratype; Va = Voucher; Loc = Locality; Sou = Source; Cd = Category designation; * = Additional host; † = Additional locality; ‡ = Category designation obtained from Ghoshroy and Caira (2001); § = Category designation obtained from Fyler and Caira (2006); ¶ = Category designation obtained in this study from original descriptions; ** = Host identification requiring confirmation. |
|---|---|---|---|---|---|---|
| Species of Host | Species of Acanthobothrium | Ht | Loc | Sou | Cd |
| A. adlardi | *Pristiophorus cirratus* (Latham, 1794) | SAM AHC 28210 | EIO, WSP | Port Stanvac, South Australia | 4§ |
| | | SAM AHC 22724, 22723 | | | |
| | A. aetiobatidis | *Aetobatus narinari* (Euphrasen, 1790) | WSA, WCA, WCA, ECA | Lifu, Loyalty Islands | 6§ |
| | | | | Baer and Euzet (1962), Goldstein (1967) | |
| | | | | Mayes et al. (1978), Southwell (1925), Baer and Euzet (1962) | |
| | | | | Campbell and Beveridge (2002) | |
| | | | | Fyler and Caira (2006) | |
| | | | | Ghoshroy and Caira (2001) | |
| | | | | Fyler and Caira (2006) | |
| | | | | Ghoshroy and Caira (2001) | |
| | | | | Fyler and Caira (2006) | |
| | | | | Ghoshroy and Caira (2001) | |
| | | | | Fyler and Caira (2006) | |
| Species of *Acanthobothrium* | Ht     | Nt, Pt or Va | Species of Host | Gd     | Loc                          | Sou                               | Cd  |
|----------------------------|--------|--------------|-----------------|--------|------------------------------|-----------------------------------|-----|
| *A. atahualpai* Marques, Brooks & Barriga, 1997 | MEPN 3029 | MNHG 22098; CNHE 3029 | Gymnura afuere (Hildebrand, 1946) | ECP, ESP | Puerto Bolivar, Provincia de El Oro, Ecuador | Marques et al. (1997a) | 1‡  |
| *A. australis* Robinson, 1965 | AMS    | AMS          | Squalus megalops (Macleay, 1881) | ENA, MED, ECA, ESA, WIO, EIO, WSP | Eden, New South Wales, Australia | Robinson (1965) | 3$  |
| *A. australis* † | NR     | SAM AHC 22696 | Squalus megalops | ENA, MED, ECA, ESA, WIO, EIO, WSP | Beachport, South Australia | Campbell and Beveridge (2002) | –   |
| *A. bajaensis* Appy & Dailey, 1973 | USNPC 72567 | USNPC 72568 | Heterodontus francisci (Girard, 1855) | ECP, ESP | San Quintin Bay, Baja California, Mexico | Appy and Dailey (1973) | 4‡  |
| *A. bajaensis* † | NR     | NR           | Heterodontus francisci | ECP, ESP | Newport Bay, California, USA | Appy and Dailey (1973) | –   |
| *A. bartonae* Campbell & Beveridge, 2002 | SAM AHC 28235 | NR            | Rhynchopterus djiddensis** | WIO, NIO | Broome, Western Australia | Campbell and Beveridge (2002) | 1§  |
| *A. batailloni* Euzet, 1955 | NR     | NR           | Myliobatis aquila (Linnaeus, 1758) | ENA, MED, ECA, ESA, WIO | Mediterranean Sea, Gulf du Lion | Euzet (1955) | 7(2)‡ |
| *A. batailloni* † | NR     | MNHNC 20015  | Myliobatis chilensis** Philippi, 1892 | ESP | Antofagasta, Chile | Carvajal-G. and Jeges-G. (1980) | –   |
| *A. batailloni* † | NR     | NR           | Myliobatis chilensis** | ESP | Coquimbo, Chile | Carvajal-G. and Jeges-G. (1980) | –   |
| *A. batailloni* † | NR     | NR           | Myliobatis chilensis** | ESP | Trujillo, Peru | Escalante-A. (1986) | –   |
| *A. benedenii* (Lönnberg, 1889) | NR     | NR           | Raja clavata Linnaeus, 1758 | ENA, MED, ECA, ESA, WIO | Mediterranean Sea | Lönnberg (1889) | 2‡  |
| Species of 
Acanthobothrium | Ht | Cd | Loc | Sou | Species of Host | Species of Host (Type) | Genus | Host (Type) | Loc | Sou |
|-------------------|----|----|-----|-----|------------------|-----------------------|-------|-------------|-----|-----|
| A. benedenii<sup>+</sup> | NR | NR | NR | NR | T. marmorata<sup>†</sup> | P. violacea<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Risso (1810) | Naples, Italy | Baer (1948) |
| A. bengalense<sup>†</sup> | NR | NR | NR | NR | P. sephen | P. sephen<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Forsskål (1775) | Nagapattinam, India | Baer and Euzet (1962) |
| A. blairi<sup>†</sup> | NR | NR | NR | NR | D. whitleyi | D. whitleyi<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Iredale (1938) | Stanley, Tasmania | Campbell and Beveridge (2002) |
| A. bobconniorum<sup>†</sup> | NR | NR | NR | NR | R. laevis | R. laevis<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Bloch & Schneider (1801) | Gove Harbor, Gulf of Carpentaria, Australia | Fyler and Caira (2010) |
| A. brachyacanthum<sup>†</sup> | USNPC 37418 | NR | NR | NR | H. say | H. say<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Lesueur (1817) | Dry Tortugas, Florida, USA | Riser (1955) |
| A. brachyacanthum<sup>+</sup> | USNPC 37418 | NR | NR | NR | B. binoculata | B. binoculata<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Gilbert (1855) | Monterey Bay, California, USA | Riser (1955) |
| A. brayi<sup>†</sup> | SAM AHC 22670 | SAM AHC 22730 | SAM AHC 22811 | SAM AHC 22812 | S. tentaculatus | S. tentaculatus<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Peters (1864) | Eastern Shoal, South Australia | Campbell and Beveridge (2002) |
| A. brevissime<sup>†</sup> | NR | NR | NR | NR | B. polyacanthus | B. polyacanthus<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Gilbert (1855) | Monterey Bay, California, USA | Riser (1955) |
| A. brevissime<sup>+</sup> | NR | NR | NR | NR | R. say | R. say<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Lesueur (1817) | Monterey Bay, California, USA | Riser (1955) |
| A. byersi | NR | NR | NR | NR | C. elongatus | C. elongatus<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Pfeffer (1868) | Monterey Bay, California, USA | Riser (1955) |
| A. byersi | NR | NR | NR | NR | C. elongatus | C. elongatus<sup>†</sup> | ENP, ECP, ESP, WSA, WWA, MED, NIO, WSP, ESP | Pfeffer (1868) | Monterey Bay, California, USA | Riser (1955) |
| Species of *Acanthobothrium* | Ht | Ni, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-----------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. brevissime*††           | NR | NR         | *Raja eglanteria* Bosc, 1800 | WCA, WNA | Gulf of Mexico, Chesapeake Bay, Virginia, USA | Campbell (1969) | – |
| *A. brevissime*††           | NR | USNPC 71349, 71350 | *Hypanus americanus* | WSA, WCA, WNA | Gulf of Mexico, Chesapeake Bay, Virginia, USA | Campbell (1969) | – |
| *A. brevissime*††           | NR | CH-MHNJIP 727 | *Myliobatis peruviensis* Garman, 1913 | ESP | Lima, Peru | Tantaleán-Vidaurre (1991) | – |
| *A. brevissime*†            | USNPC 9008 | USNPC 60178 (neotype) | *Hypanus say* | WSA, WCA, WNA | Gulf of Mexico, Chesapeake Bay, Virginia, USA | Campbell (1969), Vardo-Zalik and Campbell (2011) | – |
| *A. bullardi* Ghoshroy & Caira, 2001 | CNHE 4045 | CNHE 4046–4047; LRP 2060–2062; USNPC 90466–90468 | *Hypanus dipterurus* (Jordan & Gilbert, 1880) | ECP | Bahía de Los Angeles, Gulf of California, Mexico | Ghoshroy and Caira (2001) | 2‡ |
| *A. bullardi*†              | NR | NR         | *Hypanus dipterurus* | ECP | Puerto Rosalia, Gulf of California, Mexico | Ghoshroy and Caira (2001) | – |
| *A. bullardi*‡              | NR | NR         | *Hypanus dipterurus* | ECP | Santa Rosalia, Gulf of California, Mexico | Ghoshroy and Caira (2001) | – |
| *A. cairae* Vardo-Zalik & Campbell, 2011 | USNPC 103801 | USNPC 103802–103814 | *Bathyfoiia centoura* (Mitchell, 1815) | WSA, WCA, WNA | Narragansett Bay off Sakonnet Point, Rhode Island, USA | Vardo-Zalik and Campbell (2011) | 3§ |
| *A. campbelli* Marques, Brooks & Monks, 1995 | MNHG 20014 | MNHG 20015–20016; HWML 38546; CNHE 3033 | *Urotrygon chilenis* (Günther, 1872) | ECP, ESP | Costa de Pajaros, Puntarenas, Costa Rica | Marques et al. (1995) | 2‡ |
| *A. campbelli*††            | NR | MEPN 3033 | *Hypanus longus* (Garman, 1880) | ECP | Puerto Huanuco, Provincia de El Oro, Ecuador | Marques et al. (1997a) | – |
| *A. cannoni* Campbell & Beveridge, 2002 | SAM AHC 28236 | SAM AHC 28237 | *Himantura uarnak* (Gmelin, 1789) | WIO, NIO, ELO, WCP | Fog Bay, Timor Sea, North Australia | Campbell and Beveridge (2002) | 4§ |
| *A. cartagenensis* Brooks & Mayes, 1980 | USNPC 75159 | NR | *Urobatis jamaicensis* (Cuvier, 1816) | WCA, WNA | Cartagena, Colombia | Brooks and Mayes (1980) | 1§ |
| Species of *Acanthobothrium* | Ht | Ni, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|------------------------------|----|--------------|-----------------|----|-----|-----|----|
| *A. cartagenensis*† | NR | CNHE 9706; HWML 101020; CHE P00061 | *Urobatis jamaicensis* | WCA, WNA | Ría Lagartos, Yucatán, Quintana Roo | Monks et al. (2015) | – |
| *A. cartagenensis*† | NR | CNHE 9706; HWML 101020; CHE P00061 | *Urobatis jamaicensis* | WCA, WNA | Isla Contoy, Quintana Roo | Monks et al. (2015) | – |
| *A. cartagenensis*† | NR | CNHE 9706; HWML 101020; CHE P00061 | *Urobatis jamaicensis* | WCA, WNA | Isla Cozumel, El Paso de los Cedros, Quintana Roo | Monks et al. (2015) | – |
| *A. cartagenensis*† | NR | CNHE 9706; HWML 101020; CHE P00061 | *Urobatis jamaicensis* | WCA, WNA | Xcalak, Quintana Roo | Monks et al. (2015) | – |
| *A. cestraciontis* (Yamaguti, 1934) | NR | NR | *Heterodontus japonicus* | WNP, WCP | Pacific Ocean, Japan | Yamaguti (1934) | 4§ |
| *A. cestraciontis*† | NR | NR | *Sphyraena japonica* | ? | Pacific Ocean, Japan | Goldstein (1967) | – |
| *A. chabahariense* Maleki, Malek & Rastgoo, 2018 | ZCUOK 100 | ZCUOK 101–112 and (SME specimen) ZCUOK 113 | *Pastinachus cf. sephen* | NIO | Chabahar coasts, the coast of the Gulf of Oman, Iran | Maleki et al. (2018) | 1¶ |
| *A. chengi* Cornford, 1974 | USNPC 72958 | USNPC 72959 | *Bathyrobia lata* (Garman, 1880) | ECP, ENA, MED, ECA, WIO, NIO, EIO, WSP, WCR, WNP | Oahu, Hawaii | Cornford (1974) | 3§ |
| *A. chilensis* Rego, Vincente & Herrera, 1968 | CHIOC 30.308 a-c | NR | *Sarda chilensis* | ? | Paita, Piura, Peru | Rêgo et al. (1968) | 3§ |
| *A. chisholmae* Campbell & Beveridge, 2002 | SAM AHC 28223 | SAM AHC 28224 | *Pastinachus sephen* | NIO | Nickol Bay, Western Australia | Campbell and Beveridge (2002) | 2§ |
| *A. cimari* Marques, Brooks & Monks, 1995 | MNHG 20017 | MNHG 20018–20020; HWML 38547 | *Hypanus longus* | ECP | Punta Morales, Puntarenas Province, Costa Rica | Marques et al. (1995) | 2‡ |
| *A. clarkeae* Campbell & Beveridge, 2002 | SAM AHC 28349 | SAM AHC 28350 | *Urolophus paximaculatus* Dixon, 1969 | EIO, WSP | Queenscliff, Victoria, Australia | Campbell and Beveridge (2002) | 1§ |
| Species of Acanthobothrium | Species of Host | Loc | Collection Details | Remarks |
|---------------------------|----------------|-----|--------------------|---------|
| A. clarkeae*† | Urolophus cruciatus (Lacepède, 1804) | EIO | SAM AHC 28243, 28244 | Campbell and Beveridge (2002) |
| A. clarkeae*† | Urolophus expansus McCulloch, 1916 | WSP | SAM AHC 28208 | Campbell and Beveridge (2002) |
| A. cleofanus | Hypanus longus | ECP | CNHE 2670 | (Monks et al. 1996) |
| A. colombianum | Aetobatus narinari | WSA, WCA, WNA, ECA | USNPC 75160, 75161 | Brooks and Mayes (1980) |
| A. confusum | Neotrygon kuhlii | WSP | NR | Baer and Euzet (1962) |
| A. coquimbensis* | Myliobatis chilensis | ESP | NMNHNC 20016 | Carvajal-G. and Jeges-G. (1980) |
| A. coronatum*† | Dipturus batis (Linnaeus, 1758) | ECA | NR | Rudolphi (1819), Baer (1948) |
| A. coronatum*† | Scyliorhinus stellaris (Linnaeus, 1758) | ECA | NR | Rudolphi (1819), Baer (1948) |
| A. coronatum*† | Torpedo marmorata | ECA | NR | Rudolphi (1819), Baer (1948) |
| A. coronatum*† | Torpedo marmorata | ECA | NR | Rudolphi (1819), Baer (1948) |
| A. correae | Mustelus mustelus (Linnaeus, 1758) | ECA | NR | Euzet (1959) |
| A. coronatum*† | Mobula tarapacana (Müller & Henle, 1841) | WNP | NR | Yoshida (1917) |
| A. coronatum*† | Aetobatus narinari | ECA | NR | Euzet (1959), MacCallum (1921) |
| A. coronatum*† | Scyliorhinus stellaris | ECA | NR | Euzet (1959), MacCallum (1921) |
| A. coronatum*† | Mustelus mustelus (Linnaeus, 1758) | ECA | NR | Euzet (1959), MacCallum (1921) |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd     | Loc                  | Sou                  | Cd       |
|------------------------------|----|--------------|----------------|--------|----------------------|----------------------|----------|
| *A. coronatum*†              | NR | NR           | *Scyliorhinus stellaris* | ENA, MED, ECA | Cardigan Bay, UK | Rees and Williams (1965) | –        |
| *A. coronatum*               | NR | NR           | *Caruscherodon carcharias* (Linnaeus, 1758) | MED | Mediterranean Sea | Goldstein (1967) | –        |
| *A. coronatum*†              | NR | MNHG 40003, 40009 | *Scyliorhinus canicula* (Linnaeus, 1758) | ENA, MED, ECA | Naples, Italy | Euzet (1959), Vardozalik and Campbell (2011) | –        |
| *A. costarricense* Marques, Brooks & Monks, 1995 | MNHG 20008 | MNHG 20009–2010; HWML 38544; CNHE 3034 | *Hypanus longus* | ECP | Punta Morales, Puntarenas Province, Costa Rica | Marques et al. (1995) | 2‡      |
| *A. costarricense*†           | NR | MEPN 3034    | *Hypanus longus* | ECP | Puerto Huatulco, Provincia de El Oro, Ecuador | Marques et al. (1997a) | –        |
| *A. crassicolle* Wedl, 1855   | NR | MNHG 40014 8877 | *Dasyatis pastinaca* | ENA, MED, ECA | Arcachon, Gironde, France | Dollfus (1926), Baer (1948), Goldstein (1967) | 3§       |
| *A. cribbi* Campbell & Beveridge, 2002 | SAM AHC 28251 | SAM AHC 28252 | *Gymnura australis* (Ramsay & Ogilby, 1886) | EIO, WSP, WCP | Gulf of Carpentaria, Northern Territory, Australia | Campbell and Beveridge (2002) | 4§       |
| *A. dasi* Ghoshroy & Caira, 2001 | CNHE 4043 | CNHE 4044; HWML 15549–15551; LRP 2051–2054; USNPC 90463–90465 | *Hypanus dipterurus* | ECP | Puertecitos, Gulf of California, Mexico | Ghoshroy and Caira (2001) | 2‡       |
| *A. dasybati* Yamaguti, 1934  | NR | NR           | *Hemipterygon abaeji* | WNP | Tarumi, Kobe, Japan | Yamaguti (1934) | 4§       |
| *A. dasybati*†               | NR | NR           | *Okamejei kenojei*† (Müller & Henle, 1841) | WNP | Maisaka, Japan | Yamaguti (1952) | –        |
| *A. dasybati*†               | NR | NR           | *Urolophus sp.*** (U. fuscus?) | ? | Hamazima, Mie, Japan | Yamaguti (1952) | –        |
| *A. dighaensis* Srivastava & Capoor, 1980 | UAA | NR           | *Pateobatis uarnacoides* (Blecker, 1852) | NIO, WCP | Digha, Orissa, India | Srivastav and Capoor (1980) | 4§       |
| *A. dollyae* Caira & Burge, 2001 | CNHE 4169 | CNHE 4170; LRP 2097–2101; USNPC 90837–90839 | *Diplobatis ommata* (Jordan and Gilbert, 1890) | ECP | Bahia de Los Angeles, Gulf of California, Mexico | Caira and Burge (2001) | 1§       |
| Species of *Acanthobothrium* | Host | Loc | Source | Species of Host | Habitat | Date | Reference |
|-------------------------------|------|-----|--------|----------------|---------|------|-----------|
| *A. dollyae*                  | NR   | NR  | NR     | Diplobatis ommata | ENA, MED, ECA, ESA, WIO | 1905 | van Beneden, 1850, Goldman (1967) |
| *A. dollyae*                  | NR   | NR  | NR     | Diplobatis ommata | ENA, MED, ECA, ESA, WIO | 1905 | van Beneden, 1850, Goldman (1967) |
| *A. dujardini*                | NR   | NR  | NR     | Raja clavata | ENA, MED, ECA, ESA, WIO | 1960 | Williams (1969) |
| *A. dujardini*                | NR   | NR  | NR     | Raja clavata | ENA, MED, ECA, ESA, WIO | 1960 | Williams (1969) |
| *A. electricolum*             | NR   | NR  | NR     | Narcine brasiliensis | EIO, WSP | 1978 | Brooks and Mayes (1978) |
| *A. elongatum*                | NR   | NR  | NR     | Rhynchobatus djiddensis | WIO, NIO | 1955 | Subhapradha (1955) |
| *A. dollyae*                  | NR   | NR  | NR     | Diplobatis ommata | ENA, MED, ECA, ESA, WIO | 1905 | van Beneden, 1850, Goldman (1967) |
| *A. dollyae*                  | NR   | NR  | NR     | Diplobatis ommata | ENA, MED, ECA, ESA, WIO | 1905 | van Beneden, 1850, Goldman (1967) |
| *A. dujardini*                | NR   | NR  | NR     | Raja clavata | ENA, MED, ECA, ESA, WIO | 1960 | Williams (1969) |
| *A. dujardini*                | NR   | NR  | NR     | Raja clavata | ENA, MED, ECA, ESA, WIO | 1960 | Williams (1969) |
| *A. electricolum*             | NR   | NR  | NR     | Narcine brasiliensis | EIO, WSP | 1978 | Brooks and Mayes (1978) |
| *A. elongatum*                | NR   | NR  | NR     | Rhynchobatus djiddensis | WIO, NIO | 1955 | Subhapradha (1955) |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-----------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. etini* Fyler & Caira, 2006 | MZUM (P) 145 | USNPC 96414–96415; LRP 3815–3824 (including cross sections and SEM specimens); MZUM (P) 146; IPMB 77.14.05 | *Urogymnus pulepis* | NIO, WCP | Off Kampung Abai, Kinabatangan River, Sabah, Malaysia | Fyler and Caira (2006) | 8§ |
| *A. filicolle* (Zschokke, 1888) Yamaguti, 1959 | NR | NR | *Torpedo marmorata* | ENA, MED, ECA, ESA | Mediterranean Sea | Zschokke (1888), Yamaguti (1959b) | 1(8)§ |
| *A. filicolle* | NR | NR | *Torpedo toreado* | ENA, MED, ECA | Mediterranean Sea | Williams (1969) | – |
| *A. floridensis* Goldstein, 1964 | USNPC 60025 | NR | *Raja eglanteria* | WCA, WNA | Gulf of Mexico and Coast of Massachusetts | Goldstein (1964) | 8(10)‡ |
| *A. floridensis* | NR | USNPC 103848–103850 | *Raja texana* Chandler, 1921 | WCA | Gulf of Mexico | Vardo-Zalik and Campbell (2011) | – |
| *A. floridensis* | NR | NR | *Raja eglanteria* | WCA, WNA | Gulf of Mexico, Chesapeake Bay, Virginia, USA, USA | Campbell (1969) | – |
| *A. fogeli* Goldstein, 1964 | USNPC 60024 | NR | *Gymnura micrura* (Bloch & Schneider, 1801) | WSA, WCA, WNA, ECA | Northeastern Gulf of Mexico, Florida | Goldstein (1964) | 1‡ |
| *A. fogeli* | NR | NR | *Gymnura micrura* | WSA, WCA, WNA, ECA | Isla Margarita, Venezuela | Mayes and Brooks (1981) | – |
| *A. fouki* Reyda & Caira, 2006 | MZUM (P) 168(h) | USNPC 97463–97464; LRP 3850–3853 (including cross sections and SEM specimens); MZUM (P) 169(p)–171(p); IPMB 77.08.14 | *Pateobatis uarnacoides* | NIO, WCP | Off Kampung Tetabuan, Sabah, Malaysia | Reyda and Caira (2006) | 1§ |
| *A. franus* Marques, Centritto & Stewart, 1997 | CNHE 3139 | USNPC 87373; CHIOC 33774a, b; CNHE 3140 | *Narcine entemedor* Jordan & Starks, 1895 | ECP | Cuajiniquil Beach, Gulf of Santa Helena, Guanacaste, Costa Rica | Marques et al. (1997b) | 5(8)‡ |
| Species of *Acanthobothrium* | Species of Host | Loc. | Date | Code | Notes |
|-------------------------------|-----------------|------|------|------|-------|
| *A. fylerae*                  | *Rhynchobatus* cf. *djiddensis* | WIO, NIO | 2015 | ZUTC 1319 | Maleki, Malek & Palm, 2015 |
| *A. gasseri*                  | *Pastinachus sephen* | NIO | 2002 | SAM AHC 28217 | Campbell & Beveridge, 2002 |
| *A. gibsoni*                  | *Rhynchobatus djiddensis* | WIO, NIO | 2002 | SAM AHC 28239 | Campbell & Beveridge, 2002 |
| *A. giganticum*               | *Gymnura micrura* | WIO, NIO, WCA, WNA, FCA | 1993 | MZUM (P) 172(h) | Sanaka, Lakshmi & Hanumantharao, 1993 |
| *A. gouldi*                   | *Müller & Henle, 1841* | WIO, NIO | 1973 | USNPC 72560 | Appy & Dailey, 1973 |
| *A. gonzalezmugaburoi*        | *Myliobatis peruvianus* | ESP, WNP | 1979 | MPM 22638 | Severino and Sarmiento (1979) |
| *A. gracile*                  | *Narke japonica* | WIO | 1952 | MPM 21239 | Yang et al. (2016) |
| *A. grandiceps*               | *Telatrygon zugei* | WCP, WNP | 1952 | MPM 21229 | Yang et al. (2016) |
| *A. guanghaiense*             | *Hemitrygon akajei* | WNP | 2005 | MPM 21229 | Yang et al. (2016) |
| Species of *Acanthobothrium* | Ht | Ni, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-------------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. halehae* Maleki, Malek & Palm, 2019 | ZCUOK 127 | ZCUOK 128–130; ZUTC Play. 1342–1343, 1 SEM voucher ZUTC Play. 1344 | *Gymnura cf. poecilura*** (Shaw, 1804) | NIO, EIO, WCP, WNP | Chabahar coast, Gulf of Oman, Iran | Maleki et al. (2019) | 1§ |
| *A. hanumantharaoi* Rao, 1977 | NR | NR | *Actomycterus nichofi* (Bloch & Schneider, 1801) | NIO, EIO, WCP, WNP | Waltair coast, Benegal Bay, India | Rao (1977) | 4§ |
| *A. herdmani* Southwell, 1912 | NR | NR | *Nearygon kuhlii*** | WSP | Ceylon Pearl Bank, Sri Lanka | Southwell (1912), Southwell (1925), Southwell (1930) | 3§ |
| *A. heterodonti* Drummond, 1937 | NR | NR | *Heterodontus portusjacksoni* (Meyer, 1793) | EIO, WSP | Lady Julia Perely Island, Victoria, Australia | Drummond (1937) | 4§ |
| *A. heterodonti†* | NR | SAM AHC 22595, 22597, 15744 | *Heterodontus portusjacksoni* | EIO, WSP | Derwent Estuary, Hobart, Tasmania | Campbell and Beveridge (2002) | – |
| *A. heterodonti†* | NR | NR | *Heterodontus portusjacksoni* | EIO, WSP | Bunbury, Western Australia | Campbell and Beveridge (2002) | – |
| *A. himanturi* Brooks, 1977 | USNPC 73963 | USNPC 73964; HWML 20260 | *Styracura schmardae* (Werner, 1904) | WCA | Caribbean Sea, La Cienaga, Magdalena, Colombia | Brooks (1977) | 1‡ |
| *A. hispidum* Riser, 1955 | USNPC 37416 | NR | *Tetronarce californica* (Ayres, 1855) | ENR, ECP, WNP | Monterey Bay, California, USA | Riser (1955) | 5‡ |
| *A. holorhini* Alexander, 1953 | USNPC 47853 | USNPC 47854 | *Myliobatis californicus* Grill, 1865 | ENR, ECP | Long Beach Harbor, California, USA | Alexander (1953) | 3‡ |
| *A. holorhini*† | NR | CHIMTDC 542 | *Myliobatis chilensis* | ESP | Callao, Peru | Rodriguez and Tantaleán-Vidaurre (1980) | – |
| *A. hypanus* Zaragoza-Tapia, Pulido-Flores & Monks, 2020 | CNHE 11255 | CNHE 11256; HWML 216261 | *Hypanus longus* | ECP | La Puntilla, Mazatlán, Sinaloa, Mexico | Zaragoza-Tapia et al. (2020) | 2‡ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|--------------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. hypermekkolpos* Fyler & Caira, 2010 | QM G232506 | QM G232507; USNPC 104280; LRP 7591, hologenophores LRP 7592–7593 | *Rhynchobatus laevis** | NIO, WNP | Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia | Fyler and Caira (2010) | 1¶ |
| *A. icelandicum* Manger, 1972 | NR | NR | *Dipterus batis* | ENA | Fafa Bay, Western coasts Iceland | Manger (1972) | 3§ |
| *A. ijimai* Yoshida, 1917 | NR | MPM 22639 | *Hemitrygon akajei* | WNP | Tokyo, Japan | Yoshida (1917), Williams (1969), Yang et al. (2016) | 4§ |
| *A. ijimai†* | NR | NR | *Hemitrygon akajei* | WNP | East China Sea, Japan | Yamaguti (1952) | – |
| *A. inbiorium* Marques, Centritto & Stewart, 1997 | CNHE 3137 | USNPC 87373; CHIOC 33753a, b; CNHE 3138 | *Narcine entemedor* | ECP | Cuajiniquil Beach, Gulf of Santa Helena, Guanacaste, Costa Rica | Marques et al. (1997b) | 5§ |
| *A. incognita* (MacCallum, 1921) Wardle & McLeod, 1952 | NR | NR | *Dasyatis pastinaca* | ENA, MED, ECA | New York Aquarium | MacCallum (1921), Southwell (1925), Williams (1969) | 2¶ |
| *A. indicum* (Subhapradha, 1955) | NR | NR | *Narcine brasiliensis** | WSA | Madras Coast, India | Subhapradha (1955), Williams (1969) | 5§ |
| *A. intermedium* Perrenoud, 1931 | NR | NR | *Dasyatis pastinaca** | ENA, MED, ECA | Tauranga, New Zealand | Perrenoud (1931) | 4§ |
| *A. jalalii* Maleki, Malek & Palm, 2013 | ZUTC 1291 | ZUTC 1292–1295; SEM voucher ZUTC 1296; IPCAS C–639; ZMB E.7559 | *Pastinachus cf. sephen** | NIO | Gulf of Oman, Iran | Maleki et al. (2013) | 1¶ |
| *A. jamesi* Maleki, Malek & Palm, 2015 | ZUTC 1328 | ZMB E.7570; SEM voucher ZUTC 1329 | *Rhynchobatus cf. djiddensis** | WIO, NIO | Persian Gulf, Iran | Maleki et al. (2015) | 1¶ |
| *A. janineae* Maleki, Malek & Palm, 2015 | ZUTC 1311 | ZUTC 1312–1316; ZMB E.7566; SEM vouchers ZUTC 1317–1318 | *Rhynchobatus cf. djiddensis** | WIO, NIO | Gulf of Oman, Iran | Maleki et al. (2015) | 1¶ |
| Species of *Acanthobothrium* | Species of Host | Loc | Cd | Segm | Ref. |
|-----------------------------|----------------|-----|----|------|------|
| *A. janneae* Fyler & Caira, 2010 | *Rhynchobatus laevis* **| Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia | QM G232502–G232505; USNPC 104279; LRP 7573–7575, cross sections of one paratype worm and voucher LRP 7576–7578, SEM holotype LRP 7579 | Ht | 18 |
| *A. jonesi* Campbell & Beveridge, 2002 | *Dasyatis* sp.** | Cape York, North Australia | SAM AHC 28227 | Cd | 68 |
| *A. karachiense* Bilqees, 1980 | *Mustelus manazo* Bleeker, 1855 | Karachi Coast, Pakistan | ZCUOK 122; ZUTC Platy. 1336–1340, 1 SEM voucher ZUTC Platy. 1341 | Ht | 48 |
| *A. kurdistanense* Maleki, Malek & Palm, 2019 | *Gymnura cf. poecilura* ** | Chabahar coast, Gulf of Oman, Iran | ZCUOK 123–127; SEM voucher ZUTC Platy. 1341 | Ht | 1 ¶ |
| *A. larsoni* Reyda & Caira, 2006 | *Pateobatis uarnacoides* | Off Kampung Terabuan, Sabah, Malaysia | MZUM (P) 176(h); USNPC 97467–97468; LRP 3860–3865 (including cross sections and SEM specimens); MZUM (P) 177(p)–180(p); IPMB 77.08.16 | Cd | 2 ¶ |
| *A. lasti* Campbell & Beveridge, 2002 | *Rhynchobatus djiddensis* ** | Broome, Western Australia | SAM AHC 28247; USNPC 28215; IPMB 77.08.16 | Ht | 2 § |
| *A. latum* Yamaguti, 1952 | *Hemitrygon akajei* | Sea of Ariake, Kyusyu, Japan | MZUM (P) | Ht | 4 § |
| *A. laurenbrownae* Campbell & Beveridge, 2002 | *Pastinachus sephen* | Nickol Bay, Western Australia | SAM AHC 28216; USNPC 103816–103819 | Ht | 1 § |
| *A. lentiginosum* Vardo-Zalik & Campbell, 2011 | *Pseudobatos lentiginosus* (Garman, 1880) | Gulf of Mexico | MPM 22637 | Ht | 1 § |
| Species of Acanthobothrium | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|---------------------------|----|-------------|----------------|----|-----|-----|----|
| A. lepidum Reyda & Caira, 2006 | MZUM (P) 181(h) | USNPC 97469; LRP 3866–3868 (including cross sections and SEM specimens); MZUM (P) 182(p)–183(p); IPMB 77.08.17 | Pateobatis uarnacoides | NIO, WCP | Off Kampung Tetabuan, Sabah, Malaysia | Reyda and Caira (2006) | 1§ |
| A. lilium Baer & Euzet, 1962 | NR | NR | Dasyatis sp.** | ? | Ceylon Pearl Bank, Sri Lanka | Baer and Euzet (1962) | 2$ |
| A. lineatum Campbell, 1969 | USNPC 71353 | USNPC 71354 | Hypanus americanus | WSA, WCA, WNA | Chesapeake Bay, Virginia, USA | Campbell (1969) | 1‡ |
| A. lintoni Goldstein, Henson & Schlicht, 1968 | USNPC 62938 | USNPC 62939 | Narcine brasiliensis** | WSA | Gulf of Mexico, Texas, USA | Goldstein et al. (1969) | 1(8,9,5)‡ |
| A. lintoni† | NR | USNPC 74851 | Narcine brasiliensis** | WSA | Gulf of Mexico, Florida, USA | Goldstein et al. (1969) | – |
| A. longipendunculata Meheswari, Sanaka, Lakshmi & Rao, 1985 | NR | NR | Himantura uarnak | WIO, NIO, EIO, WCP | Waltair coast, India | Maheswari et al. (1985) | 6§ |
| A. lusamientos Severino & Verano, 1980 | CH-MHNJP 342 | CH-MHNJP 343, 343a | Sympterygia brevicaudata (Cope, 1877) | ECP, ESP | Callao, Lima, Peru | Severino and Verano (1980) | 7¶ |
| A. maccanthium Southwell, 1925 | NR | NR | Urogymnus sp.** | ? | Madras Coast, India | Southwell (1925) | 6§ |
| A. macrocephalum Wang & Yang, 2001 | MPM 21231 | NR | Hemitrygon abajei | WNP | Xiamen, Fujian, China | Wang and Yang (2001), Yang et al. (2016) | 4§ |
| A. macrocephalum† | MPM 21231 | MPM 21232; SYSU 20140620-1-7 | Hemitrygon abajei | WNP | Off Guanghai Port, Guangdong, China | Yang et al. (2016) | – |
| A. macrocephalum† | NR | NR | Hemitrygon abajei | WNP | Sanya Fishing Port, Sanya, Hainan, China | Yang et al. (2016) | – |
| A. maculatum Riser, 1955 | USNPC 37417 | NR | Myliobatis californicus | ENP, ECP | Monterey Bay, California, USA | Riser (1955) | 6(3)‡ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-------------------------------|----|--------------|----------------|----|-----|-----|----|
| *A. magnum* Euzet, 1959       | NR | NR           | *Pteroplatytrygon violacea* | ENP, ECP, ESP, WSA, WCA, WNA, ENA, MED, ECA, ESA, WIO, NIO, EIO, WSP, WCP, WNP | Mediterranean Sea, France | Euzet (1959) | 4§ |
| *A. makranense* Maleki, Malek & Palm, 2019 | ZCUOK 130 | ZCUOK 131–135; ZUTC Play. 1345–1350, 1 SEM voucher ZCUOK 139, 1 SEM voucher ZUTC Play. 1350 | *Gymnura cf. poecilura* | NIO, EIO, WCP, WNP | Chabahar coast, Gulf of Oman, Iran | Maleki et al. (2019) | 1§ |
| *A. manteri* Hassan, 1983     | IHAHE S1051/A | IHAHE S1051/B | *Pastinachus sephlen* | NIO | Mediterranean Sea, Egypt | Hassan (1983) | 5§ |
| *A. margieae* Fyler, 2011     | NMNS 6356–001 | NMNS 6356–002, 6356–003, 6356–004, 6356–005, 6356–006, 6356–007; LRP 7468–7477; USNPC 103274 | *Orectolobus japonicus* Regan, 1906 | WNP, WCP | Off Penghu Island, East China Sea, Magong, Taiwan | Fyler (2011) | 8§ |
| *A. marplatensis* Ivanov & Campbell, 1998 | MLP 4025 | MLP 4026; USNMPC 87475; NHMUK 1998.2.10.1-2 | *Atlantoraja castelnaui* (Miranda Ribeiro, 1907) | WSA | Mar del Plata, Buenos Aires, Argentina | Ivanov and Campbell (1998) | 1‡ |
| *A. marquesi* Rodríguez-Ibarra, Pulido-Flores, Violante-González & Monks, 2018 | CNHE 10554 | CNHE 10555, 10556; HWML 139377–139384; CHE P00061–P00063 | *Actobatus cf. narinari* | WSA, WCA, WNA, ECA | Laguna de Términos, Ciudad del Carmen, Campeche, Mexico | Rodríguez-Ibarra et al. (2018) | 3¶ |
| *A. marquesi*† | NR | NR | *Actobatus cf. narinari* | WSA, WCA, WNA, ECA | Champotón, Campeche, Mexico | Rodríguez-Ibarra et al. (2018) | – |
| *A. martini* Campbell & Beveridge, 2002 | SAM AHC 28213 | SAM AHC 28214 | *Myliobatis teneracaudatus* Hector, 1877 | EIO, WSP | Bunbury, Western Australia | Campbell and Beveridge (2002) | 1§ |
| Species of *Acanthobothrium* | Ht       | Nt, Pt or Va | Species of Host               | Gd   | Loc                  | Sou             | Cd          |
|----------------------------|----------|--------------|-------------------------------|------|----------------------|-----------------|-------------|
| *A. maryanskii* Caira & Burge, 2001 | CNHE 4171 | CNHE 4172; LRP 2012, 2013; USNPC 90840, 90841 | *Diplobatis ommata* | ECP | Loreto, Gulf of California, Mexico | Caira and Burge (2001) | 5§          |
| *A. marymichaelorum* Twohig, Caira & Fyler, 2008 | MZUM(P) 699(H) | MZUM(P) 700(0)–702(P); SBC P-00028; USNPC 100700; LRP 4162–4164 (whole mount), 4167–4168 (cross sections) | *Brevityryn walga* (Müller & Henle, 1841) | NIO | Off Sematan, Sarawak, Malaysia | Twohig et al. (2008) | 1§          |
| *A. marymichaelorum* | NR       | NR           | *Brevityryn walga* | NIO | Off Mukah, Sarawak, Malaysia | Twohig et al. (2008) | –           |
| *A. masiniae* Fyler & Caira, 2006 | MZUM (P) 147 | USNPC 96416–96417; LRP 3825–3835 (including cross sections and SEM specimens); MZUM (P) 148; IPMB 77.14.06 | *Urogymnus polylepis* | NIO, WCP | Kampung Abai, Kinabatangan River, Sabah, Malaysia | Fyler and Caira (2006) | 2§          |
| *A. mathiasi* Euzet, 1959 | NR       | NR           | *Mustelus mustelus* | ENA, MED, ECA, ESA | Sète, France | Euzet (1959) | 1§          |
| *A. mathiasi* | NR       | NR           | *Mustelus canis* (Mitchill, 1815) | WNA, WCA, WSA | Sète, France | Euzet (1959) | –           |
| *A. mattaylo* Fyler & Caira, 2010 | QM G232508 | Hologenophore USNPC 104281 | *Rhynchobatus laevis* | NIO, WNP | Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia | Fyler and Caira (2010) | 4§          |
| *A. micracantha* Yamaguti, 1952 | NR       | MPM 22635, 22636 | *Hemistrygon abajci* | WNP | Nagasaki, East China Sea, Japan | Yamaguti (1952), Yang et al. (2016) | 4§          |
| *A. micracantha* | NR       | NR           | *Gymnura micrura* | WSA, WCA, WNA, ECA | Nagasaki, East China Sea, Japan | Yamaguti (1952) | –           |
| *A. micracantha* | NR       | NR           | *Telatrygon zugai* | WCP, WNP | Nagasaki, East China Sea, Japan | Yamaguti (1952) | –           |
| *A. microcephalum* Alexander, 1953 | USNPC 47852 | NR           | *Myliobatis californicus* | ENP, ECP | Long Beach Harbor, California, USA | Alexander (1953) | 4‡          |
| Species of *Acanthobothrium* | Ht | Ni, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-----------------------------|----|--------------|----------------|----|-----|-----|----|
| *A. minus* | MNHN HEL 76, Th 180 | MNHN HEL 77, Th 181, HEL 78, Th 182, HEL 79, Th 183; NHMUK 2009.2.10.1-2 | *Raja asterias* Delaroche, 1809 | ENA, MED | Cap Djinet, Algérie | Tazerouti et al. (2009) | 2§ |
| *A. minus†* | NR | NR | *Raja asterias* | ENA, MED | | | |
| *A. minus†* | NR | NR | | | | | |
| *A. minusculus* | MEPN 3030 | MNHG 22099; HWML 39178; CNHE 3030 | *Urolophus tumbesensis* (Chirichigno F. & McEachran, 1979) | ECP | Puerto Hualtaco, Provincia de El Oro, Ecuador | Marques et al. (1997a) | 1‡ |
| *A. monksi* | MEPN 3031 | MNHG 22100; HWML 39179; CNHE 3031 | *Actobatus narinari*** | WSA, WCA, WNA, ECA | Puerto Jelí, Provincia de El Oro, Ecuador | Marques et al. (1997a) | 1‡ |
| *A. mooreae* | SAM AHC 28209 | SAM AHC 22665, 22718, 28265 | *Trygonorrhina fasciata* | WSP | Northhaven, South Australia | Campbell and Beveridge (2002) | 2§ |
| *A. mujibi* | SPUK 2001 (syntype) | | *Mustelus manazo* | NIO, WCP, WNP | Karachi Coast, Pakistan | Bilqees (1980) | 2§ |
| *A. musculosum* (Baer, 1948) | NR | NR | *Pteroplatyrygon violacea* | ENP, ECP, ESP, WSA, WCA, WNA, ENA, MED, ECA, ESA, WIO, NIO, EIO, WSP, WCR, WNP | New Zealand | Baer (1948), Euzet (1959), Yamaguti (1959a), Williams (1969) | 4§ |
| *A. mykometactata* | DZCJ | NR | *Aetomyloaena maculata* (Gray, 1834) | NIO, WCP, WNP | Madras Coast, India | Srivastav et al. (1995) | 4§ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc                                      | Sou                        | Cd |
|-----------------------------|----|-------------|----------------|----|-----------------------------------------|----------------------------|----|
| *A. nanogravidum* Zschoche, Caira & Fyker, 2011 | QM G232166 | QM G232167–G23217, cross sections QM G232171, G23217; USNPC 104103; LRP 7480–7483, cross sections LRP 7486–7491, SEM LRP 7484–7485, egg mounts LRP 7492–7493 | *Pastinachus ater* (Macleay, 1883) | WIO, NIO, EIO, WSP, WCP | Gulf of Carpentaria off Weipa, Queensland, Australia. | Zschoche et al. (2011) | 15 |
| *A. nicoyaense* Brooks & McCorquodale, 1995 | USNPC 84477 | USNPC 84388; MNHG 18255 | *Aetobatus narinari* | WSA, WCA, WNA, ECA | Punta Morales, Golfo de Nicoya, Costa Rica | Brooks and McCorquodale (1995) | 1† |
| *A. ningdense* Yang, Sun, Zhi, Iwaki, Reyda & Yang, 2016 | MPM 21226 | MPM 21227, 21228; SYSU 201211113-1-3, 20141002-1-27 | *Hemitrygon akajei* | WNP | Fuhai aquatic market, Ningde, Fujian Province, China | Yang et al. (2016) | 45 |
| *A. ningdense*† | NR | NR | *Hemitrygon akajei* | WNP | Off Wanjichi aquatic wholesale market, Taizhou, Zhejiang Province, China | Yang et al. (2016) | – |
| *A. ningdense*† | NR | NR | *Hemitrygon akajei* | WNP | 8th Seafood Market, Xiamen, Fujian Province, China | Yang et al. (2016) | – |
| *A. ningdense*† | NR | NR | *Hemitrygon akajei* | WNP | Guanghai Port, Taishan, Guangdong Province, China | Yang et al. (2016) | – |
| *A. ningdense*† | NR | NR | *Hemitrygon akajei* | WNP | Sanya Fishing Port, Sanya, Hainan Province, China | Yang et al. (2016) | – |
| *A. obuncus* Marques, Brooks & Barriga, 1997 | MEPN 3032 | MNHG 22101; HWML 39180; CNHE 3032, 3167 | *Hypanus longus* | ECP | Puerto Hualtaco, Provincia de El Oro, Ecuador | Marques et al. (1997a) | 6‡ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-----------------------------|----|--------------|----------------|----|-----|-----|----|
| *A. ocallaghani* Campbell & Beveridge, 2002 | SAM AHC 28202 | SAM AHC 28203 | *Appicotrema vincentiana* | EIO | Musgrave Shoal, South Australia | Campbell and Beveridge (2002) | 2§ |
| *A. ocallaghani* Campbell & Beveridge, 2009 | QM 231345 | QM G231346–231347; USNPC 101957–101958; LRP 4317–4318; cross sections QM 231349, QM G231348; SEM LRP 4319–4320, 4327–4328, hologenophores LRP 4321, LRP 4322 | *Urogymnus acanthobothrium* Last, White & Kyne, 2016 | WSP, WCP | Arafura Sea, east of Wessel Islands, Northern Territory, Australia. | Fyler et al. (2009), Caira and Jensen (2017) | 1§ |
| *A. odonoghuei* Campbell & Beveridge, 2002 | SAM AHC 22699 | SAM AHC 22699 | *Urolophus expansus* | EIO | Holdfast Bay, South Australia | Campbell and Beveridge (2002) | 1§ |
| *A. odonoghuei*† | NR | NR | *Urolophus lobatus* McKay, 1966 | EIO | Esperance, Western Australia | Campbell and Beveridge (2002) | – |
| *A. olseni* Dailey & Mudry, 1968 | USNPC 71216 | NR | *Pseudobatos productus* (Ayres, 1854) | ENP, ECP | Newport Beach, California, USA | Dailey and Mudry (1968) | 2‡ |
| *A. olseni*† | NR | NR | *Pseudobatos planiceps* (Garman, 1880) | ECP, ESP | Lima, Chorrillos, Peru | Iannace et al. (2011) | – |
| *A. olseni*† | NR | NR | *Urobatis halleri* (Cooper, 1863) | ENP, ECP | Anaheim Bay, California, USA | Appy and Dailey (1973) | – |
| *A. olseni*† | NR | NR | *Urobatis halleri* | ENP, ECP | Puerto Peñasco, Sonora, Mexico | Friggens and Brown (2005) | – |
| *A. omanense* Maleki, Malek & Palm, 2019 | ZCUOK 117 | ZCUOK 118–122; ZUTC Play. 1330–1334, 1 SEM voucher ZUTC Play. 1335 | *Gymnura cf. poecilura* | NIO, EIO, WCP, WNP | Chabahar coast, Gulf of Oman, Iran | Maleki et al. (2019) | 1§ |
| *A. omanense* | NR | NR | *Gymnura cf. poecilura* | NIO, EIO, WCP, WNP | Bandar Abbas, Persian Gulf, Iran | Maleki et al. (2019) | – |
| *A. parviuncinatum* Young, 1954 | USNPC 49095 | NR | *Urobatis halleri* | ENP, ECP | San Diego Bays, California, USA | Young (1954) | 8‡ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|------------------------------|----|--------------|----------------|----|-----|-----|----|
| *A. parviuncinatum*          | NR | NR           | Gymnura marmorata (Cooper, 1864) | ECP | San Diego Bays, California, USA | Young (1954) | – |
| *A. parviuncinatum†*         | NR | NR           | Urobatis halleri | ENP, ECP | Puerto Peñasco, Sonora, Mexico | Friggens and Brown (2005) | – |
| *A. parvum* Manger, 1972     | NR | NR           | Dipturus hatis | ENA | Fuxa Bay, Western coasts Iceland | Manger (1972) | 6§ |
| *A. paulum* Linton, 1890     | NR | USNPC 07683, 35882, 71351, 71352 | Bathytoshia centrowa | WSA, WCA, WNA | Woods Hole, Massachusetts, USA | Linton (1890), Vardo-Zalik and Campbell (2011) | 1(8,9,5)§ |
| *A. paulum*†                 | NR | NR           | Raja eglanteria | WCA, WNA | Chesapeake Bay, Virginia, USA | Campbell (1969) | – |
| *A. paulum*†                 | NR | NR           | Hypopus americanus | WSA, WCA, WNA | Chesapeake Bay, Virginia, USA | Campbell (1969) | – |
| *A. pearsoni* Williams, 1962 | NR | NR           | Orectolobus maculatus (Bonnaterre, 1788) | EIO, WSP | Hastings Point NSW, Australia | Williams (1962), Campbell and Beveridge (2002) | 1§ |
| *A. persicum* Maleki, Malek & Palm, 2019 | ZCUOK 135 | ZCUOK 136–137; ZUTC Play. 1351–1352, 1 SEM voucher ZCUOK 142, 1 SEM voucher ZUTC Play. 1353 | Gymnura cf. poecilura** | NIO, EIO, WCP, WNP | Bandar Abbas, Persian Gulf, Iran | Maleki et al. (2019) | 1§ |
| *A. peruvienne* Reyda, 2008  | USNPC 99945 | USNPC 99946; LRP 4108–4111 (including whole mounts and SEM specimens); MZUSP 6393a–6393b; MHNP 2335 | Potamotrygon motoro (Müller & Henle, 1841) | WSA, WCA | Madre de Dios River at Boca Manu, Madre de Dios Department, Peru | Reyda (2008) | 1(8)§ |
| *A. pichelinae* Campbell & Beveridge, 2002 | SAM AHC 28229 | SAM AHC 28230 | Myliobatis tenuicaudatus | EIO, WSP | Devonport, Tasmania | Campbell and Beveridge (2002) | 4§ |
| *A. pichelinae†*              | NR | NR           | Myliobatis tenuicaudatus | EIO, WSP | Bunbury, Western Australia | Campbell and Beveridge (2002) | – |
| Species of Acanthobothrium | Ht   | Nt, Pt or Va | Species of Host | Gd   | Loc               | Sou                          | Cd |
|---------------------------|------|-------------|-----------------|------|-------------------|------------------------------|----|
| *A. pintanensis* Wang, 1984 | NR   | NR          | *Neotrygon kuhlii* | WSP  | Fujian Province, China | Wang (1984)                  | 4§ |
| *A. polytesticularis* Wang & Yang, 2001 | PRLXU | NR         | *Squalus* sp.**  | ?    | Xiamen, Fujian, China | Wáng and Yang (2001)          | 4§ |
| *A. ponticum* Léon-Borcea, 1934 | NR   | NR          | *Raja clavata*   | ENA, MED, ECA, ESA, WIO | Agigéa, Black Sea            | Léon-Borcéa (1934)           | 2¶ |
| *A. ponticum* *†* | NR   | NR          | *Dasypis pastinaca* | ENA, MED, ECA | Agigéa, Black Sea      | Léon-Borcéa (1935)           | –  |
| *A. popi* Fyler, Caira & Jensen, 2009 | QM G231350 | QM G231351–G231352; USNPC 101959–101960; LRP 4323–4324; cross sections QM G231353; SEM LRP 4329–4330, 4325–4326, hologenophores LRP 4331, 4332 Urognymus acanthobothrium | WSP, WCP | Arafura Sea, east of Wessel Islands, Northern Territory, Australia. | Fyler et al. (2009), Caira and Jensen (2017) | 2¶ |
| *A. ppdeleoni* Zaragoza-Tapia, Pulido-Flores & Monks, 2020 | CNHE 11253 | CNHE 11254; HWML 216260 Hypanus ditterurus | ECP | Bahía de Chamele, Jalisco, Mexico | Zaragoza-Tapia et al. (2020) | 2¶ |
| *A. psammobati* Carvajal & Goldstein, 1969 | USNPC 71357 | USNPC 71358 Psammobatis scobina (Philippi, 1857) | ESP | South Pacific Ocean, between Papudo and Talcahuano, Chile | Carvajal-G. and Goldstein (1969) | 5‡ |
| *A. psammobati* *†* | NR   | CH-MHNJP 342a, 342b Sympterygia brevicaudata | ECP, ESP | Callao, Lima, Peru | Tantaleán-Vidaurre (1991) | –  |
| *A. puertecitense* Caira & Zahner, 2001 | CNHE 4175 | CNHE 4176; USNPC 90843; LRP 2105–2106 Heterodontus francisci | ECP, ESP | Puertecitos, Gulf of California, Mexico | Caira and Zahner (2001) | 4¶ |
| *A. puntarenasense* Marques, Brooks & Monks, 1995 | MNHG 20005 | MNHG 20006–20007; HWML 38543, CNHE 4176 Hypanus longus | ECP | Punta Morales, Puntarenas Province, Costa Rica | Marques et al. (1995) | 2‡ |
| *A. quadripartitum* Williams, 1968 | NR   | NR          | *Leucosyn naevus* (Müller & Henle, 1841) | ENA, MED, ECA | North Sea, off Aberdeen | Williams (1968) | 2§ |
| Species of *Acanthobothrium* | Ht | Ni, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-------------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. quinonesi* Mayes, Brooks & Thorson, 1978 | USNPC 74804 | USNPC 74805; HWML 74806 | *Potamotrygon magdalenae* (Duméril, 1865) | WCA | Magdalena River, Cienaga Jobo, vicinity of San Cristobal, Bolivar, Colombia | Mayes et al. (1978) | 5‡ |
| *A. quinonesi*† | NR | NR | *Potamotrygon yepezi* Castex & Castello, 1970 | WCA | Lake Maracaibo area near El Congo and Represa de Tule, Rio Cachiri, Zulia, Venezuela | Brooks et al. (1981) | – |
| *A. rajaebatis* (Rudolphi, 1810) Euzet, 1959 | NR | NR | *Dipturus batis*** | ENA | Mediterranean Sea | Rudolphi (1810) | 5§ |
| *A. rajaebatis*† | NR | NR | *Dipturus oxyrinchus* (Linnaeus, 1758) | ENA, MED, ECA | Sète, France | Euzet (1959) | – |
| *A. rajaebatis*† | NR | NR | *Rostroraja alba* (Lacepède, 1803) | ENA, MED, ECA, ESA, WIO | Sète, France | Euzet (1959) | – |
| *A. rajaebatis*† | NR | NR | *Rostroraja alba* | ENA, MED, ECA, ESA, WIO | Lacépède, France | Euzet (1959) | – |
| *A. rajaebatis*† | NR | NR | *Dipturus batis*** | ENA | Sète, France | Euzet (1959) | – |
| *A. rajaebatis*† | NR | NR | *Dipturus batis*** | ENA | Roscoff, France | Euzet (1959) | – |
| *A. rajivi* Ghoshroy & Caira, 2001 | CNHE 4038 | CNHE 4039; HWML 15552; LRP 2055–2056; USNPC 90461 | *Hypanus dipterurus* | ECP | Puertecitos, Gulf of California, Mexico | Ghoshroy and Caira (2001) | 2‡ |
| *A. ramiroi* Ivanov, 2005 | MACN-Pa 412/1-4 | USNPC 92521 | *Potamotrygon motoro* | WSA, WCA | Rio Colastiné, Santa Fé, Argentina | Ivanov (2005) | 4§ |
| *A. ramiroi*† | NR | NR | *Potamotrygon motoro* | WSA, WCA | Rio Coronda, Santa Fé, Argentina | Ivanov (2005) | – |
| *A. regoi* Brooks, Mayes & Thorson, 1981 | USNPC 75709 | USNPC 75710; HWML 21012, 21013 | *Potamotrygon hystrix* (Müller & Henle, 1841) | WSA | Orinoco River Dfra, Orinoco River near Los Castillos, Venezuela | Brooks et al. (1981) | 5‡ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-----------------------------|----|-------------|-----------------|----|-----|-----|----|
| *A. regoi*†                 | NR | NR          | *Potamotrygon falkneri* Castex & Maciel, 1963 | WSA | Paraná River, Brazil | Lacerda et al. (2008) | – |
| *A. regoi*†                 | NR | NR          | *Potamotrygon motoro* WSA, WCA | Paraná River, Brazil | Lacerda et al. (2008) | – |
| *A. rhinobati* Alexander, 1953 | USNPC 47858 | USNPC 47859 | *Pseudobatos productus* ENP, ECP | Santa Monica Harbor, California, USA | Alexander (1953) | 9(5)‡ |
| *A. rhinobati*†              | NR | NR          | *Pseudobatos productus* ENP, ECP | Ocean Park Pier, California, USA | Alexander (1953) | – |
| *A. robertsoni* Campbell & Beveridge, 2002 | SAM AHC 28197 | SAM AHC 22590, 22591, 22592, 22667, 22714 | *Trygonorrhina fasciata* | WSP | Middleton, South Australia | Campbell and Beveridge (2002) | 3§ |
| *A. robertsoni*†             | NR | SAM AHC 28257 | *Pristiophorus cirratus* | EIO, WSP | Port Stanvac, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | NR          | *Aptychootrema vincentiana* | EIO | North Haven, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | NR          | *Aptychootrema vincentiana* | EIO | Goolwa, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | NR          | *Dentiraja cerva* (Whitley, 1939) | EIO, WSP | Port Stanvac, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | NR          | *Dentiraja cerva* | EIO, WSP | Holdfast Bay, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | SAM AHC 28260 | *Urolophus bucculentus* Macleay, 1884 | EIO, WSP | Rapid Head, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | SAM AHC 22699 | *Urolophus expansus* | EIO | Holdfast Bay, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†             | NR | SAM AHC 28256 | *Urolophus lobatus* | EIO | Esperance, Western Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni†              | NR | NR          | *Trygonorrhina fasciata* | WSP | Outer Harbour, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni†              | NR | NR          | *Trygonorrhina fasciata* | WSP | North Haven, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni†              | NR | NR          | *Trygonorrhina fasciata* | WSP | Port Stanvac, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni†              | NR | NR          | *Trygonorrhina fasciata* | WSP | Goolwa, South Australia | Campbell and Beveridge (2002) | – |
| Species of *Acanthobothrium* | Ht | Nr, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-------------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. robertsoni*†              | NR | NR          | *Trygonorrhina fasciata* | WSP | Port Vincent, South Australia | Campbell and Beveridge (2002) | – |
| *A. robertsoni*†              | NR | NR          | *Trygonorrhina fasciata* | WSP | Queenscliff, Victoria, Australia | Campbell and Beveridge (2002) | – |
| *A. robustum* Alexander, 1953 | USNPC 47856 | USNPC 47857 | *Pseudobatos productus* | ENP, ECP | Long Beach Harbor, California, USA | Alexander (1953) | 4‡ |
| *A. robustum*†                | NR | NR          | *Pseudobatos planiceps* | ECP, ESP | Trujillo, Peru | Escalante-A. (1986) | – |
| *A. rodmani* Fyler, Caira & Jensen, 2009 | QM G231354 | QM G231355–G231357; USNPC 101961–101963; LRP 4333–4335; cross sections QM G231359 G231358; cross sections LRP 4564–4569, 4563, longitudinal sections 4560–4562, 4559; SEM LRP 4336–4339, hologenophores LRP 4340, 4341 | *Urogymnus acanthobothrium* | WSP, WCP | Arafura Sea, east of Wessel Islands, Northern Territory, Australia. | Fyler et al. (2009), Caira and Jensen (2017) | 6¶ |
| *A. rohdei* Campbell & Beveridge, 2002 | SAM AHC 28233 | SAM AHC 28234 | *Urolophus lobatus* | EIO | Esperance, Western Australia | Campbell and Beveridge (2002) | 1§ |
| *A. romanowi* Fyler, Caira & Jensen, 2009 | QM G231360 | QM G231361–231363; USNPC 101964–101966; LRP 4342–4344; cross sections QM G231365, G231364; cross sections LRP 4351–4356, SEM LRP 4345–4348, hologenophores LRP 4350, 4349. | *Urogymnus acanthobothrium* | WSP, WCP | Arafura Sea, east of Wessel Islands, Northern Territory, Australia. | Fyler et al. (2009), Caira and Jensen (2017) | 1¶ |
| *A. rotundum* Subhapradha, 1955 | NR | NR | *Rhynchobatus djiddensis* | WIO, NIO | Madras Coast, India | Subhapradha (1955) | 4§ |
| Species of Host | Species of | Host | Loc | Cd | Source |
|----------------|-----------|------|-----|----|--------|
| A. royi        | Ht        | Diplobatis ommata | Loreto, Gulf of California, Mexico | ECP 2104 | USNPC 90842 | \( A. royi \) Caira & Burge (2001) |
| A. rubrum      | Ht        | Mustelus manazo   | Karachi Coast, Pakistan | NIO, WCP | WNP | \( A. rubrum \) Bilqees (1980) |
| A. saliki      | Ht        | Urogymnus polylepis | Kariba, Shal, Malaysia | NIO, WCP | IPMB 77.14.07 | \( A. saliki \) Fyler & Caira (2006) |
| A. santarosaliense | Ht       | Heterodontus mexicanus | Santa Rosalia, Gulf of California, Mexico | ECP 2107 | USNPC 90844 | \( A. santarosaliense \) Caira and Zahner (2001) |
| A. satyanarayanaraoi | Ht   | Glaucostegus granulatus | Waltair coast, India | DZAUW | NR | \( A. satyanarayanaraoi \) Sanaka et al. (1993) |
| A. schalli     | Ht        | Mustelus canis    | Gulf of Mexico | USNPC 103820 | USNPC 103821–103826 | \( A. schalli \) Vardo-Zalik and Campbell (2011) |
| A. semnovesiculum | Ht    | Pastinachus sephen | Gulf of Mexico | USNPC 103820 | USNPC 103821–103826 | \( A. semnovesiculum \) Caira and Burge (2001) |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-------------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. sinaloensis* Zaragoza-Tapia, Pulido-Flores & Monks, 2020 | CNHE 11257 | CNHE 11258; HWML 216262 | *Hypanus longus* | ECP | La Puntilla, Mazatlan, Sinaloa, Mexico | Zaragoza-Tapia et al. (2020) | 2§ |
| *A. soberoni* Ghoshroy & Caira, 2001 | CNHE 4040 | CNHE 4041–4042; HWML 15548; LRP 2057–2059; USNPC 90462 | *Hypanus dipterurus* | ECP | Puertecitos, Gulf of California, Mexico | Ghoshroy and Caira (2001) | 6‡ |
| *A. soberoni†* | NR | NR | *Hypanus dipterurus* | ECP | Bahia de Los Angeles, Gulf of California, Mexico | Ghoshroy and Caira (2001) | – |
| *A. soxiae* Zaragoza-Tapia, Pulido-Flores, Violante-Gonzalez & Monks, 2019 | CNHE 11136 | CNHE 11137; HWML 139978; CHE P00081 | *Narcine entemedor* | ECP | Bahia de Acapulco, Playa Las Hamacas, Guerrero, Mexico | Zaragoza-Tapia et al. (2019) | 2§ |
| *A. southwelli* Subhapradha, 1955 | NR | NR | *Rhinobatos schlegeli* Müller & Henle, 1841 | WNP | Madras Coast, India | Subhapradha (1955) | 1§ |
| *A. sphaera* Maleki, Malek & Palm, 2013 | ZUTC 1298 | ZUTC 1299–1307; SEM vouchers ZUTC 1308–1309; IPCAS C-641; ZMB E7560 | *Pastinachus cf. sephen* Müller & Henle, 1841 | NIO | Persian Gulf, Iran | Maleki et al. (2013) | 2§ |
| *A. stefaniae* Franzese & Ivanov, 2018 | MACN-Pa 624 | MACN-Pa 625/1–6, 626/1–3, 627/1, 628/1–2; IPCAS C-786; LRP 9403–9410 | *Discopyge tschudii* Heckel, 1846 | ESP, WSA | Coastal waters off Mar Chiquita City, Buenos Aires Province | Franzese and Ivanov (2018) | 1§ |
| *A. stefaniae†* | NR | NR | *Discopyge tschudii* Heckel, 1846 | ESP, WSA | Coastal waters off Villa Gesell, Argentina | Franzese and Ivanov (2018) | – |
| *A. stefaniae†* | NR | NR | *Discopyge tschudii* Heckel, 1846 | ESP, WSA | Off San Clemente del Tuyu, Argentina | Franzese and Ivanov (2018) | – |
| *A. stefaniae†* | NR | NR | *Discopyge tschudii* Heckel, 1846 | ESP, WSA | Off Camarones, Argentina | Franzese and Ivanov (2018) | – |
| *A. stevensi* Campbell & Beveridge, 2002 | SAM AHC 28198 | SAM AHC 28199 | *Trygonorrhina fasciata* | WSP | Marion Bay, South Australia | Campbell and Beveridge (2002) | 2§ |
| Species of *Acanthobothrium* | Ht    | Nt, Pt or Va | Species of Host | Gd     | Loc                        | Sou                        | Cd |
|------------------------------|-------|--------------|-----------------|--------|----------------------------|----------------------------|----|
| *A. stevensi*†               | NR    | NR           | *Trygonorrhina fasciata* | WSP    | Goolwa, South Australia    | Campbell and Beveridge (2002) | –  |
| *A. stevensi*†               | NR    | NR           | *Trygonorrhina fasciata* | WSP    | Coorong, Australia         | Campbell and Beveridge (2002) | –  |
| *A. tasajerasi* Brooks, 1977 | USNPC 73961 | USNPC 73962; HWML 20261 | *Styracura schmardae* | WCA    | Caribbean Sea, La Cienaga, Magdalena, Colombia | Brooks (1977) | 2‡ |
| *A. tasajerasi*†             | NR    | NR           | *Hypanus guttatus* (Bloch & Schneider, 1801) | WSA, WCA | Lake Maracaibo, Venezuela | Mayes and Brooks (1981) | –  |
| *A. terezae* Rego & Dias, 1976 | CHIOC 31.215c | CHIO 10.847, 10.994, 31.412a-b, 31.215a-b | *Potamotrygon motoro* | WSA, WCA | Rio Salobra, Mato Grosso, Brazil | Régo and Luna Dias (1976) | 4‡ |
| *A. tetabuanense* Reyda & Caira, 2006 | MZUM (P) 184(h) | USNPC 97470–97471; LRP 3869–3873 (including cross sections and SEM specimens); MZUM (P) 185(p)–186(p); IPMB 77.08.18 | *Pateobatis sarnacoides* | NIO, WCP | Off Kampung Tetabuan, Sabah, Malaysia | Reyda and Caira (2006) | 2§ |
| *A. thomasae* Campbell & Beveridge, 2002 | SAM AHC 28201 | SAM AHC 22676 | *Aptychotrema vincentiana* | EIO    | Musgrave Shoal, South Australia | Campbell and Beveridge (2002) | 2§ |
| *A. thomasae*†               | NR    | NR           | *Aptychotrema vincentiana* | EIO    | Cowell, Australia          | Campbell and Beveridge (2002) | –  |
| *A. tortum* (Linton, 1916) Baer & Euzet, 1962 | NR    | NR           | *Aetobatus narinari* | WSA, WCA, WNA, ECA | Woods Hole, Massachusetts, USA | Linton (1916) | 3‡ |
| *A. tortum*†                 | NR    | NR           | *Aetobatus narinari* | WSA, WCA, WNA, ECA | Caimaré Chico, Gulf of Venezuela | Mayes and Brooks (1981) | –  |
| *A. tortum*†                 | NR    | USNPC 70494  | *Aetobatus narinari* | WSA, WCA, WNA, ECA | Cape Haze Marine Laboratory, Sarasota, Florida | Campbell (1970) | –  |
| *A. triacis* Yamaguti, 1952  | NR    | NR           | *Triakis scyllium* Müller & Henle, 1839 | WNP    | Hamazima, Mie, Japan       | Yamaguti (1952) | 4§ |
| *A. tripartitum* Williams, 1969 | NR    | NR           | *Raja microcelata* Montagu, 1818 | ENA, ECA | English Channel, Plymouth   | Williams (1969) | 2§ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|------------------------------|----|--------------|----------------|----|-----|-----|----|
| *A. ulmeri* Vardó-Zalik & Campbell, 2011 | USNPC 103830 | USNPC 103831–103837, 103839, 103842, 103846 | *Raja texana* | WCA | Gulf of Mexico | Vardó-Zalik and Campbell (2011) | 1§ |
| *A. unilatens* Alexander, 1953 | USNPC 47855 | NR | *Myliobatis californicus* | ENP ECP | Long Beach Harbor, California, USA | Alexander (1953) | 7(2)‡ |
| *A. urogymini* (Hornell, 1912) Southwell, 1925 | NR | NR | *Urogymnus asperimiss* (Bloch & Schneider, 1801) | ECA, WIO, NIO, EIO, WSP, WCP, WNP | Gulf of Mannar, India | Hornell (1912), Southwell (1925) | 2§ |
| *A. urolophi* Schmidt, 1973 | USNPC 72284 | USNPC 72284 | *Trygonoptera testacea* Müller & Henle, 1841 | WSP | Glenelg Beach near Adelaide, South Australia | Schmidt (1973) | 1§ |
| *A. urolophi*†† | NR | NR | *Urolophus paucimaculatus* | EIO, WSP | Devonport, Tasmania | Campbell and Beveridge (2002) | – |
| *A. urotrygoni* Brooks & Mayes, 1980 | USNPC 75162 | USNPC 75163; HWML 20917 | *Urobatis venezuelae* Schultz, 1949 | WCA | Cartagena, Colombia | Brooks and Mayes (1980) | 2‡ |
| *A. urotrygoni*†† | NR | NR | *Hypanus guttatus* | WSA, WCA | Lake Maracaibo, Venezuela | Mayes and Brooks (1981) | – |
| *A. urotrygoni*†† | NR | NR | *Hypanus guttatus* | WSA, WCA | Isla Margarita, Venezuela | Mayes and Brooks (1981) | – |
| *A. vargasi* Marques, Brooks & Monks, 1995 | MNHG 20011 | MNHG 20012–20013; HWML 38545 | *Hypanus longus* | ECP | Punta Morales, Puntarenas Province, Costa Rica | Marques et al. (1995) | 2‡ |
| *A. vidalii* Zaragoza-Tapia, Pulido-Flores, Vielante-Gonzalez & Monks, 2019 | CNHE 11134 | CNHE 11135; HWML 139979-139981; CHE P00082 | *Narcine entemedor* | ECP | Bahía de Acapulco, Playa Las Hamacas, Guerrero, Mexico | Zaragoza-Tapia et al. (2019) | 6¶ |
| *A. walkeri* Campbell & Beveridge, 2002 | SAM AHC 28219 | SAM AHC 28220 | *Pastinachus sephen*** | NIO | Nickol Bay, Western Australia | Campbell and Beveridge (2002) | 2§ |
| *A. walkairensis* Uma Maheswari, Sanaka, Vijaya Lakshmi & Hanumantha Rao, 1987 | NR | NR | *Himantura uarnak* | WIO, NIO, EIO, WCP | Waltair coast, India | Maheswari et al. (1987) | 3§ |
| *A. wedli* Robinson, 1959 | NR | NR | *Zeareja nasuta* (Müller & Henle, 1841) | WSP | Petone Beach, New Zealand | Robinson (1959) | 4§ |
| Species of *Acanthobothrium* | Ht | Nt, Pt or Va | Species of Host | Gd | Loc | Sou | Cd |
|-------------------------------|----|-------------|----------------|----|-----|-----|----|
| *A. wedli*†                   | NR | NR          | *Zeamja nasuta* | WSP| Portobello, Otago Harbour, New Zealand | Robinson (1959) | – |
| *A. wedli*†                   | NR | NR          | *Zeamja nasuta* | WSP| South Island, off Lyttelton, New Zealand | Campbell and Beveridge (2002) | – |
| *A. westi* Vardo-Zalik & Campbell, 2011 | USNPC 103841 | USNPC 103838, 103840, 103843–103845, 103847 | *Raja texana* | WCA | Gulf of Mexico | Vardo-Zalik and Campbell (2011) | 1ʃ |
| *A. woodsholei* Baer, 1948    | NR | MNHG 40028 (syntype) | *Bathytoshia centoura* | WSA, WCA, WNA | Woods Hole, Massachusetts, USA | Baer (1948), Vardo-Zalik and Campbell (2011) | 2(7)ʃ |
| *A. woodsholei*†              | NR | NR          | *Bathytoshia centoura* | WSA, WCA, WNA | Western North Atlantic | Goldstein (1964) | – |
| *A. xiamenensis* Yang & Lin, 1994 | NR | NR          | *Rynchobatus djiddensis*** | WIO, NIO | Xiamen, South Fujian, China | Yang (1994) | 5ʃ |
| *A. zainali* Fyler & Caira, 2006 | MZUM (P) 151 | USNPC 96420–96422; LRP 3844-3849 (including cross sections and SEM specimens); MZUM (P) 152–153; IPMB 77.14.08 | *Urogymnus polyepis* | NIO, WCP | Off Kampung Abai, Kinabatangan River, Sabah, Malaysia | Fyler and Caira (2006) | 1ʃ |
| *A. zapterycum* Ostrowski de Nuñez, 1971 | MACN-Pa 214/1 | NR | *Zapteryx brevirostris* (Müller & Henle, 1841) | WSA | Mar del Plata, Buenos Aires, Argentina | Ostrowski de Nuñez (1971) | 2ʃ |
| *A. zapterycum*†              | NR | MACN-Pa 214/1-2, 214/4–5, 629/1, 630/1–3, 631/1–4, 632/1–4; IPCAS C-787; LRP 9411–9417 | *Zapteryx brevirostris* | WSA | Coastal waters off Villa Gesell, Argentina | Franzese and Ivanov (2018) | – |
| *A. zapterycum*†              | NR | NR          | *Zapteryx brevirostris* | WSA | La Lucila del Mar, Argentina | Franzese and Ivanov (2018) | – |
| *A. zapterycum*†              | NR | NR          | *Zapteryx brevirostris* | WSA | Puerto Quequén, Argentina | Franzese and Ivanov (2018) | – |
| Species of Acanthobothrium | Ht       | Nt, Pt or Va | Species of Host                  | Gd       | Loc                          | Sou                        | Cd     |
|-----------------------------|----------|--------------|----------------------------------|----------|------------------------------|----------------------------|--------|
| *A. zapterycum*†            | NR       | NR           | *Zapteryx brevirostris*           | WSA      | WSA, Puerto Pirámides, Argentina | Franzese and Ivanov (2018) | –      |
| *A. zimmeri* Fyler, Caira & Jensen, 2009 | QM G231366 | QM G231367–G231369; USNPC 101967–101969; LRP 4357–4358; cross sections QM G231371, G231370; cross sections LRP 4364–4366, SEM LRP 4359–4361, hologenophores LRP 4363, 4362 | *Urogymnus acanthobothrium* | WSP, WCP | Arafura Sea, east of Wessel Islands, Northern Territory, Australia. | Fyler et al. (2009), Caira and Jensen (2017) | 15     |
| *A. zschokkei* Baer, 1948   | MHNG 88/39 | NR           | Torpille (common name)**         | ?        | Naples, Italy                | Baer (1948)                | 6§     |
| *A. zschokkei*†             | NR       | NR           | *Torpilla marmorata*              | ENA, MED, ECA, ESA | Adriatic Sea, Mediterranean Sea | Goldstein (1967)            | –      |
| *A. zschokkei*†             | NR       | NR           | *Torpillo torpedo*                | ENA, MED, ECA | Sète, France                 | Euzet (1959)               | –      |
| *A. zschokkei*†             | NR       | NR           | *Torpillo torpedo*                | ENA, MED, ECA | Adriatic Sea, Mediterranean Sea | Goldstein (1967)            | –      |
Results

The information obtained from the metadata analysis (Table 1) is comprised of 336 reports of the 201 valid species of *Acanthobothrium*. The list includes the type host of each species, type locality, and additional hosts and/or localities. Five of the elasmobranchs that were reported as hosts of *Acanthobothrium* were only identified to genus and four others are reported as “cf.” (= similar to) (see Table 1).

The type localities where species of *Acanthobothrium* have been reported is shown in Figure 1. The currently known diversity of sharks comprises 517 species (34 families); of these, 19 species of sharks (eight families) have been reported to be parasitized by species of *Acanthobothrium* (Fig. 2). Eighteen of the 201 valid species have been described from sharks. The families of sharks that have the highest number of reports are Orectolobidae (three different species of *Acanthobothrium*), Heterodontidae (five species) and Triakidae (six species) (Fig. 2B). In contrast, currently known diversity of rays comprises 637 species (26 families); of these, 95 species (18 families) have been reported to be parasitized by species of *Acanthobothrium* (Fig. 3). Of the 201 valid species of *Acanthobothrium*, 182 have been described from rays. The families of rays that have the highest number of reports are Rajidae (20 species of *Acanthobothrium*) and Dasyatidae (70 species) (Fig. 3B).

Species of *Acanthobothrium* are not evenly grouped in the different categories. In Category 1 there are 55 species, 44 in Category 2, 19 in Category 3, 37 in Category 4, 17 in Category 5, 14 in Category 6, four in Category 7, four in Category 8, and three in Category 9. Although there is a Category 10, species in that category also are in grouped with those in Category 8 because their characteristics are thought to fall into both categories (Table 1). The categories of four species of *Acanthobothrium* were classified as unknown (“?”) because the original descriptions do not have sufficient information for assignment in one of the ten categories (Table 1).

Discussion

Currently, 517 species of sharks have been described worldwide with 3.7% (19 of the 517 species) have been reported as hosts for species of *Acanthobothrium* (Fig. 2C). In contrast, 637 species of rays have been described with 14.9% (95 of the 637 species) have been reported as hosts for species of *Acanthobothrium* (Fig. 3C). Estimates of cestode diversity in elasmobranchs discussed by Caira (2011) assumes that the fauna of cestodes of a species of elasmobranchs does not vary substantially across in its distribution. Knowledge of life cycles are essential in understanding the distribution of species of *Acanthobothrium*; however, for this study it is assumed that the distribution of adults of these parasites normally is limited to that of its normal definitive host. Thus, it is hypothesized that the limits of the distribution of the host limits the species of its parasites to the same biogeographic regions proposed for the distribution of elasmobranchs by Last et al. (2016b). It is recognized that an infected elasmobranch
Figure 2. Families of sharks: A number of species of sharks per family B number of species of sharks parasitized by species of *Acanthobothrium*. Note: The first number within parentheses corresponds to the number of species of shark that have been reported as hosts of *Acanthobothrium* and the second is the number of species that have been described from that Family C percentage of species of shark reported to be parasitized within the total number of families of sharks- note: Red color = parasitized; Blue color = not parasitized.

could move outside of the region where it has been designated, but until an extension to its distribution has been reported, it must be assumed that the normal distribution for each species of parasite also is that same designated region. The information in the table will be subject to future research, not forgetting that there is a lack of knowledge of the life cycle of the species of *Acanthobothrium*; a partial life cycle of a single species
Figure 3. Families of rays: A number of species of rays per family B number of species of rays parasitized by species of *Acanthobothrium*. Note: The first number within parentheses corresponds to the number of species of ray that have been reported as hosts of *Acanthobothrium* and the second is the number of species that have been described from that Family C percentage of species of rays reported to be parasitized within the total number of families of rays- note: Red color = parasitized; Blue color = not parasitized.

has been reported (Holland and Wilson 2009). Publication of molecular sequences for more species will provide new discoveries in this subject.

The information in the Figures 1 and 4 indicates that there is an absence of reports from several regions of the world, such as ECA, ESA, WIO, ARC, and SOC. According to the percentages of species of elasmobranchs that have been reported as hosts of species of *Acanthobothrium*, we can infer that there are still many new species of *Acanthobothrium* to be discovered. In the GenBank database records, molecular sequences
Metadata analysis of *Acanthobothrium* in elasmobranchs

of only 16 of the 201 species of *Acanthobothrium* have been reported. However, more molecular information about species of *Acanthobothrium* is required for future analyses, both for identification and life cycle studies; these would provide more solid information for delimiting distributions.

In Table 1, *Acanthobothrium chilensis* Rêgo, Vicente & Herrera, 1968, was included for reference, although it was described from a fish, *Sarda chilensis* (Cuvier, 1832) (Perciformes: Scombridae) (see Rêgo et al. 1968). Extensive recent studies of this species of fish (Chero et al. 2016; Luque et al. 2016) failed to report *A. chilensis*; there is only the report by Rêgo et al. (1968). The report of the host for this species of *Acanthobothrium* likely is an accidental infection and not a normal host.

According to Fyler et al. (2009) and Franzese and Ivanov (2018), species of *Acanthobothrium* appear to exhibit oioxenous specificity for their elasmobranch hosts. In the present metadata analysis, for species exclusively in elasmobranchs, 83% of the species of *Acanthobothrium* show remarkable host specificity for their definitive host, and thus, should be considered to be an oioxenous species. In contrast, 34 of the 200

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**Figure 4.** Number of species of *Acanthobothrium* reported from elasmobranchs in each biogeographic region (Last et al. 2016b).
species (17%) of *Acanthobothrium* have been reported in more than one species of elasmobranch (Table 1). However, with the metadata analysis of the distribution of the hosts and the reports of the species of *Acanthobothrium*, 45 of the type specimens of *Acanthobothrium* require confirmation of the host (Table 1) because some appear to be problematic identifications and other hosts were reported as “cf.” or only as an unidentified member of a particular genus. In addition, there are reports of species of *Acanthobothrium* that suggest misidentification of the parasites; these should be reevaluated in future studies. To mention obvious cases, *A. batailloni* has been reported from the Mediterranean Sea and from the Pacific coast of Peru and Chile and *A. brevissime* has been reported from the Gulf of Mexico and the Pacific coast of Peru.

The categorical method developed by Ghoshroy and Caira (2001) was proposed in order to delimit the number of taxonomic comparisons when describing new species. Using the method of Ghoshroy and Caira (2001), which focused only on species from the Americas, Fyler and Caira (2006) later applied the same methodology to biodiversity data for species from other regions; those works are augmented by this study. Of the 201 known species of *Acanthobothrium*, 13 have been classified in more than one category (see category designations in Table 1) because some characteristics of those species overlap with those of more than one category (see descriptions found in Zschokke 1888; Linton 1890; Baer 1948; Alexander 1953; Euzet 1955; Riser 1955; Yamaguti 1959; Goldstein 1964; Williams 1969; Goldstein et al. 1969; Appy and Dailey 1973; Severino and Sarmiento 1979; Marques et al. 1997; Reyda 2008). This does not decrease the usefulness of the categorical method as a tool for the initial stages in identification.

Having more information, such as molecular sequences, could solve some problems in identification, such as the two cases mentioned above. A species of *Acanthobothrium* that has been assigned to more than one category suggests that the categories still need some refining, or it is an example of cryptic species that cannot be distinguished without molecular information. However, molecular information cannot replace morphological descriptions of species. One reason is the lack of material for sequencing of the vast majority of already-known species. Morphology also augments molecular data in studies of the phylogeny of platyhelminths (Zamparo et al. 2001; Littlewood 2008). A complete phylogenetic hypothesis based on total evidence (morphological and molecular data) such as that of Littlewood (2008) for any major group of cestodes is still distant. Until that time, a categorical method provides the easiest and most direct method for selection of a group of species similar to a new species of *Acanthobothrium*. This updated database includes the category designation for each species described to date will be an important tool for the future taxonomic studies.

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