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Changes to the nomenclature of the skates (Chondrichthyes: Rajiformes)

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Abstract

In the course of the NSF-funded project "Jaws and Backbone: Chondrichthyan Phylogeny and a Spine for the Vertebrate Tree of Life", morphological and molecular data were collected for a huge number of species (including type specimens). Molecular studies using mitochondrial and nuclear markers with dense taxon sampling corroborate that the skates consist of four main family-level groups, i.e. Anacanthobatidae, Arhynchobatidae, Gurgesiellidae and Rajidae. The *Rays of the World* book followed this subdivision of skates resulting in several nomenclatural decisions at both supraspecific and species levels, which are described and discussed in the present paper. These nomenclatural changes include: 1) resurrection of the family Gurgesiellidae, comprising all eight species of *Cruriraja*, eight species of *Fenestraja* and three species of *Gurgesiella*; 2) supraspecific changes to anacanthobatid nomenclature, i.e. elevation of subgenus *Schroederobatis* to generic level and resurrection of *Springeria* from subgeneric rank as a valid genus-level taxon; 3) provisional assignment of members of two undefined genus-level taxa, the "North Pacific Assemblage" and the "Amphi-American Assemblage"; 4) reassignment of species to the genus *Dentiraja*; 5) resurrection of *Dipturus intermedius* as a valid species from synonymy with *D. batis*; 6) resurrection of the tribe Pavorajini McEachran, 1984; and 7) erection of two new tribes, Bathyrajini (type genus *Bathyraja*) and Crurirajini (type genus *Cruriraja*). Furthermore, an annotated checklist of rajiform species is provided to explain major nomenclatural changes and place the list in context with other contemporary lists.

Key words: Rajiformes, skates, nomenclatural changes, genera, species, checklist.

Introduction

A key objective of a 5-year, NSF-funded project ("Jaws and Backbone: Chondrichthyan Phylogeny and a Spine for the Vertebrate Tree of Life") was to investigate diversity in the chondrichthyan fishes and provide an inventory of species. Possibly the most challenging part of this task involved an investigation of the skates (Rajiformes), which comprise almost half of all batoid fishes. As part of the Tree of Life project, one of us (PL) travelled to museums globally to re-examine types and key specimens, and obtain images, for the compilation of skate chapters in the *Rays of the World* book. These data were supplemented by long-term datasets acquired by the co-authors (J. McEachran, B. Séret, M. Stehmann, and PL) and summarised in the skate chapters. The Tree of Life project also involved molecular analyses (NADH2 gene and mitochondrial genome) including data for more than half of the world's extant skate species (Yang *et al*., unpubl.). These projects yielded new information at all taxonomic levels and these findings are combined herein with those of a comprehensive study of the group conducted concurrently by Weigmann (2016), with an update by Weigmann (in press). These investigations, along with those conducted by other contemporary leaders in the field (M. de Carvalho, D. Ebert, H. Ishihara, C. Jeong, J. McEachran, B. Séret, M. Stehmann) have led to the description of several new species in recent times, including 4 specifically for the ray book.

Studies by Naylor *et al*. (2012a,b) using broad taxon coverage for the NADH2 gene, Aschliman *et al*. (2012) using both mitochondrial and nuclear genes, and more recent studies by Naylor *et al*. (in press) and Yang *et al*. (unpubl.), using the mitochondrial genome and nuclear markers for even denser taxon sampling, corroborate that the skates consist of four main family-level groups. The *Rays of the World* (Last *et al*., in press a) family contributions, i.e. Anacanthobatidae (Séret

et al., in press), Arhynchobatidae (Last *et al*., in press b), Gurgesiellidae (Weigmann *et al*., in press) and Rajidae (Last *et al*., in press c), followed this subdivison of the skates resulting in the nomenclatural decisions at both supraspecific and species levels discussed below. An annotated checklist of species is provided to explain major nomenclature changes and place the list in context with other contemporary lists (i.e. Compagno, 2005; Weigmann, 2016).

Supraspecific changes to skate nomenclature

Resurrection of the family Gurgesiellidae de Buen, 1959

Familial structure of the skates (order Rajiformes *sensu* Naylor *et al*., 2012a) has been the subject of much discussion in recent decades. Based on a morphological analysis, the group was considered to consist of a single family by McEachran & Dunn (1998) comprised of 5 tribes: Amblyrajini, Aryhchobatini, Gurgesiellini, Rajini and Riorajini. In preliminary work for a proposed catalogue of rays of the world, Compagno (1999) divided the order into three families: Anacanthobatidae, Arhynchobatidae and Rajidae. Naylor *et al*. (2012a,b), using a molecular analysis based on the NADH2 gene, recovered the families Arhynchobatidae and Rajidae, but *Cruriraja* Bigelow & Schroeder, 1948 fell outside these groups and was well divergent from the Anacanthobatidae (see Naylor *et al*., 2012a: Figure 2.9; Naylor *et al*., 2012b: Figure 77). *Cruriraja* grouped as the sister to the Arhynchobatidae, and *Sinobatis* Hulley, 1973 grouped as the sister to a larger group containing the rest of these skates. In the past, the phylogenetic classification of *Cruriraja* (from latin *crus* = leg or limb and skate genus *Raja* Linnaeus; type species *Cruriraja atlantis* Bigelow & Schroeder, 1948) has changed frequently. *Cruriraja* was originally placed in the family Rajidae by Bigelow & Schroeder (1948). This classification was adopted by, e.g. Wallace (1967), Hulley (1986) and Carvalho *et al*. (2006). However, *Cruriraja* was placed in its own family Crurirajidae by Hulley (1972a) based on characters of the pelvic girdle and clasper structure. Later, species of the families Anacanthobatidae and Crurirajidae were combined in the family Anacanthobatidae without a reason given by Compagno (1999). This placement was followed by, e.g. Ebert & Compagno (2007), Last & Séret (2008) and Last & Stevens (2009), who justified the placement by the joint possession of leg-like anterior pelvic-fin lobes in all species. However, skates of the genus *Cruriraja* morphologically differ greatly from anacanthobatid legskates (Figure 1).

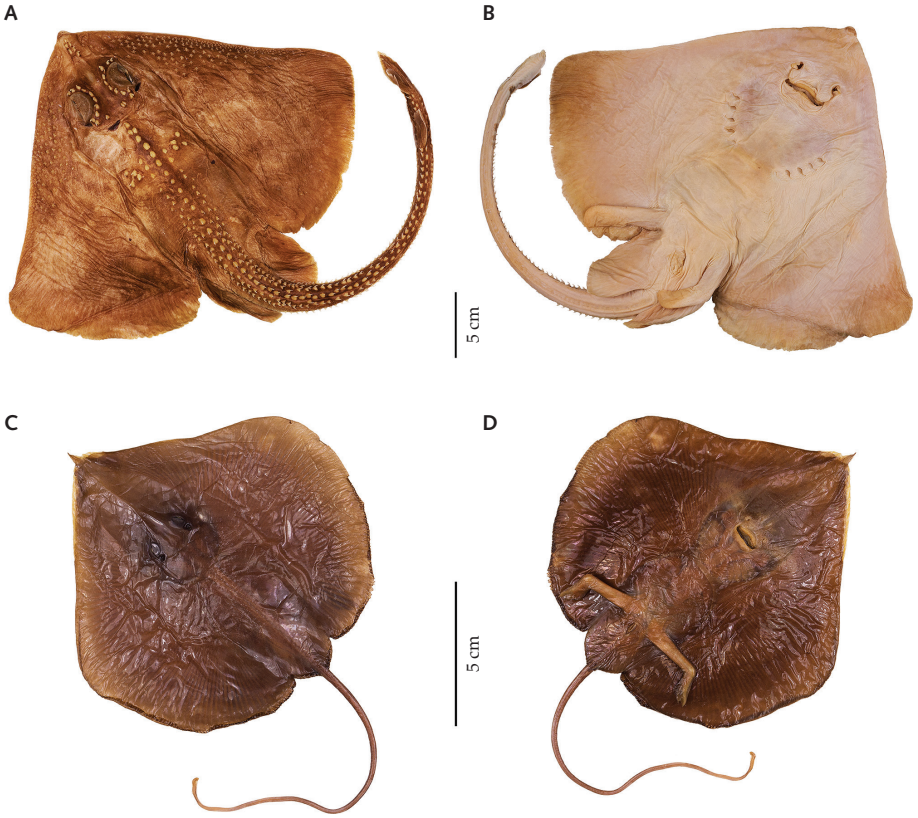

Figure 1: Comparison of the external morphology of *Cruriraja* and anacanthobatids. Adult female 532 mm TL (ZMH 105118) of *Cruriraja hulleyi* Aschliman, Ebert & Compagno, 2010 in (A) dorsal and (B) ventral views, as well as juvenile female 234.5 mm TL (ZMH 25928) of *Indobatis ori* (Wallace, 1967) in (C) dorsal and (D) ventral views.

The differences include firm, thick skin in *Cruriraja* (*vs*. soft, thin skin in anacanthobatids), a solid tail (*vs*. a thin, cord-like tail), the presence of two dorsal fins, except for one aberrant specimen of ZMH 122862 with only one dorsal fin (*vs*. no dorsal fins), and numerous thorns on the dorsal surface (*vs*. largely naked dorsally). The absence of thorns in the Anacanthobatidae was expressed also in the etymology of the family name (Weigmann *et al*., 2014a). Furthermore, in *Cruriraja* species the disc has somewhat angular outer corners (*vs*. rounded outer corners in anacanthobatids), the snout is rather short and stout (*vs*. at least moderately long and delicate), the mesopterygia of the pectoral skeleton are clearly better developed, the scapulocoracoid has fewer and larger postventral fenestrae, and the pelvic girdle has much shorter prepelvic processes (Figure 2; see also Weigmann *et al*., 2014a).

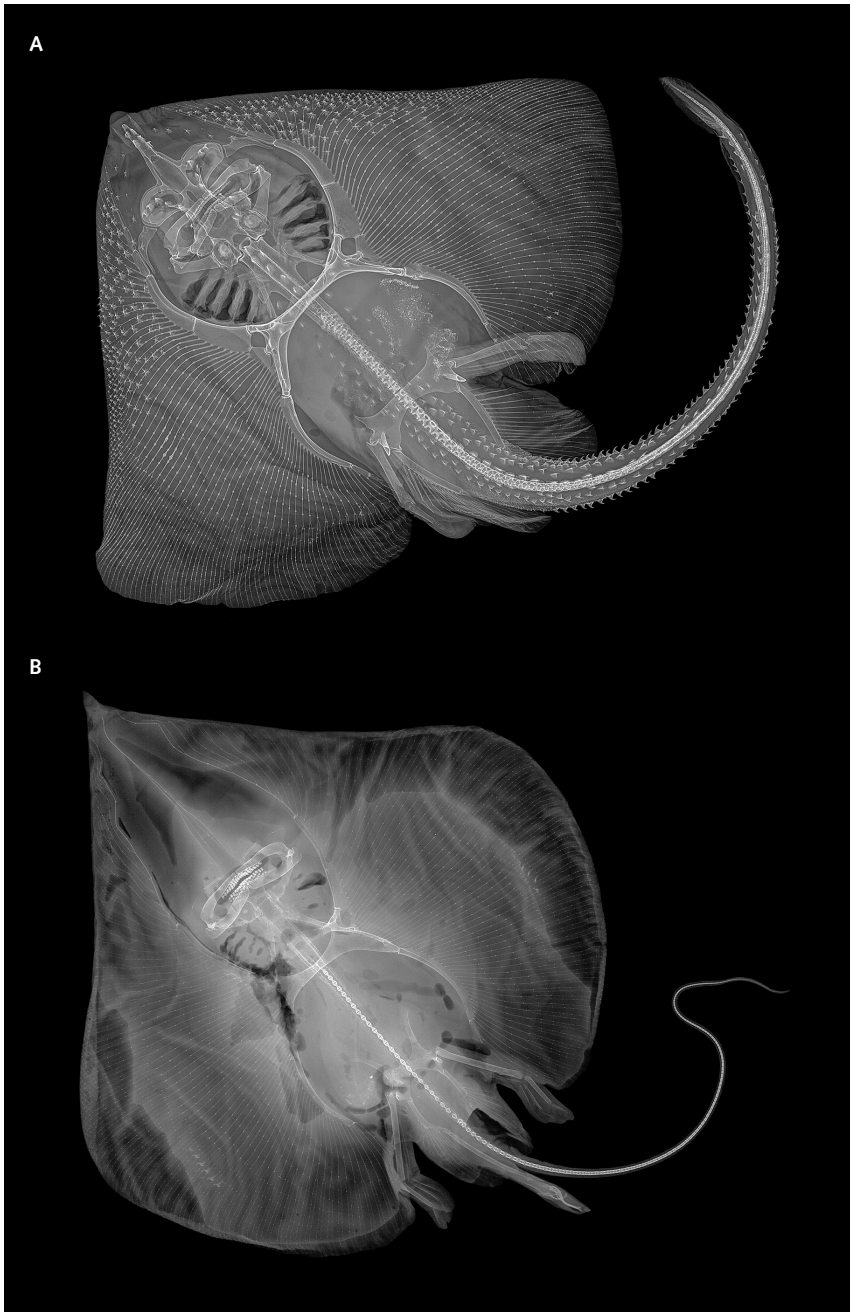

Figure 2: Comparison of the skeletal morphology of *Cruriraja* and anacanthobatids. Radiographs in dorsal total views: (A) adult female 532 mm TL (ZMH 105118) of *Cruriraja hulleyi* Aschliman, Ebert & Compagno, 2010; (B) adult male 425 mm TL (ZMH 25926) of *Indobatis ori*.

Based on the numerous differences, Weigmann *et al*. (2014a) removed *Cruriraja* from the Anacanthobatidae, placing it within its own family Crurirajidae following Hulley (1972a). This classification was adopted by van der Laan *et al*. (2014), Ebert & van Hees (2015) and Weigmann (2016). The latter reference, however, indicated that unpublished data from the Tree of Life project suggested placement of *Cruriraja* in the family Gurgesiellidae de Buen, 1959, together with the genera *Fenestraja* McEachran & Compagno, 1982 and *Gurgesiella* de Buen, 1959. The external morphologies of the latter two genera are shown in Figure 3.

Very recent molecular studies (Naylor *et al*., in press; Yang *et al*., unpubl.) have also provided compelling data supporting the resurrection of the family Gurgesiellidae. However, McEachran & Compagno (1979) had earlier discussed the validity of the monotypic families Gurgesiellidae and Pseudorajidae Bigelow & Schroeder, 1954 and revealed that genera *Gurgesiella* and *Pseudoraja* Bigelow & Schroeder, 1954 share five derived characters unique within the order (as suborder Rajoidei). Nevertheless, the Gurgesiellidae and Pseudorajidae had previously been recognized to be distinct families based on the structure of the pelvic girdle, neurocranium and hyomandibular cartilage (Hulley, 1972b). McEachran & Dunn (1998) later again placed these genera in separate families: i.e. *Gurgesiella* (Rajidae) and *Pseudoraja* (Arhynchobatidae). Although McEachran & Compagno's proposal that these genera should be placed together in the Pseudorajidae has credibility based on their original findings and reassignment of *Gurgesiella*, no fresh tissues are available for *Pseudoraja*, nor is an adult male available for clasper examination (J. McEachran, pers. comm.). In the absence of such critical information, Gurgesiellidae is provisionally resurrected as the name of this family-level taxon pending definitive information on *Pseudoraja*. The family comprises 8 species of *Cruriraja*, 8 species of *Fenestraja*, and 3 species of *Gurgesiella* (Weigmann, 2016; Weigmann *et al*., in press).

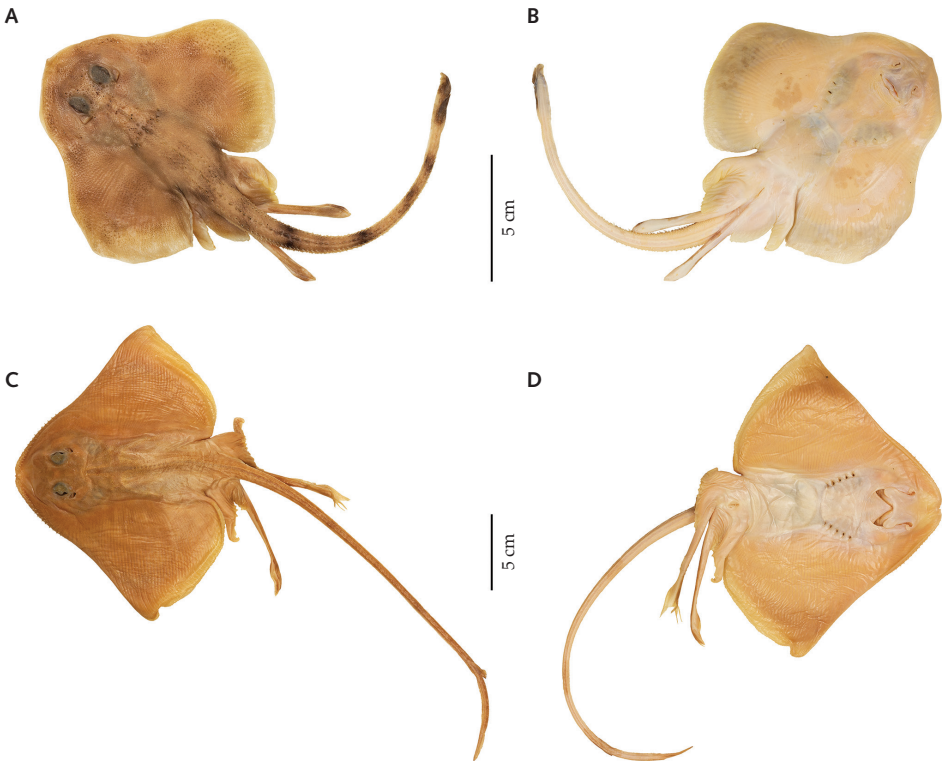

Figure 3: External morphology of *Fenestraja* and *Gurgesiella*. Adult male 232 mm TL (ZMH 119851) of *Fenestraja plutonia* (Garman, 1881) in (A) dorsal and (B) ventral views, as well as adult male holotype 424 mm TL (ZMH 25046) of *Gurgesiella dorsalifera* McEachran & Compagno, 1980 in (C) dorsal and (D) ventral views.

Supraspecific changes to anacanthobatid nomenclature

The family Anacanthobatidae and the type genus *Anacanthobatis* were erected by von Bonde & Swart (1923) for *Leiobatis marmoratus* (type species, designated with lectotype by Hulley, 1973) and *L. dubius* n. spp. from South Africa. Subsequently, a second anacanthobatid genus was described, i.e. *Springeria* Bigelow & Schroeder, 1951 with the newly described type species *S. folirostris*. *Springeria* was later redefined by Hulley (1973) as a subgenus of *Anacanthobatis*, along with the erection of two new subgenera, *Schroederobatis* and *Sinobatis*, and the definition of subgenus *Anacanthobatis* von Bonde & Swart, 1923.

All four subgenera were defined based on differences in external and skeletal clasper morphology. The differences were described in detail by Hulley (1973) and updated by Weigmann *et al*. (2014a) and Stehmann & Weigmann (2016). *Sinobatis* was elevated to generic level by Last & Séret (2008) based on differences in clasper morphology. As such differences are considered to be diagnostic of genera also in other rajiform families, elevation of subgenera *Schroederobatis* and *Springeria* to generic level was recommended by Last & Séret (2008), but not formally performed. Subsequently, Weigmann *et al*. (2014a) erected a new genus, *Indobatis* Weigmann, Stehmann & Thiel, 2014, for *Anacanthobatis ori* (Wallace, 1967) due to strong differences in the formerly unknown external and skeletal clasper morphology, clearly distinguishing this genus from all other described anacanthobatid genera and subgenera.

Considering the extent of differences in external and skeletal clasper characters between all anacanthobatid genera and subgenera (Hulley, 1973; Weigmann *et al*., 2014a; Stehmann & Weigmann, 2016), the subgenus *Schroederobatis* is herein elevated to generic level and *Springeria* is resurrected from subgeneric rank as a valid genus-level taxon.

Provisional assignment of members of two undefined genus-level taxa, the "North Pacific Assemblage" and the "Amphi-American Assemblage"

In a classification of the Rajidae based on a morphology-based phylogenetic analysis, McEachran & Dunn (1998) recognised 8 genus-level taxa within the tribe Rajini, including two un-named taxa, *Raja* "North Pacific Assemblage" and *Raja* "Amphi-American Assemblage".

The *Raja* "North Pacific Assemblage" contained 6 species: *R.* "North Pacific Assemblage" *binoculata* Girard, 1855; *R.* "North Pacific Assemblage" *rhina* Jordan & Gilbert, 1880; *R.* "North Pacific Assemblage" *inornata* Jordan & Gilbert, 1881; *R.* "North Pacific Assemblage" *stellulata* Jordan & Gilbert, 1880; *R.* "North Pacific Assemblage" *pulchra* Liu, 1932; and *R.* "North Pacific Assemblage" *cortezensis* McEachran & Miyake, 1988. The genus *Beringraja* was later erected by Ishihara *et al*. (2012) for *R. binoculata* and *R. pulchra* based on egg capsule morphology. Molecular analyses for the Chondrichthyan Tree of Life project (Yang *et al*., unpubl.) have provided strong support for recognition of a supraspecific group including all 6 species of the "North Pacific Assemblage" (no molecular data are available for *R. cortezensis*) in the genus *Beringraja* within the tribe Rajini.

The *Raja* "Amphi-American Assemblage" is a morphologically variable group comprising 7 species: *R.* "Amphi-American Assemblage" *eglanteria* Bosc, 1800; *R.* "Amphi-American Assemblage" *ackleyi* Garman, 1881; *R.* "Amphi-American Assemblage" *equatorialis* Jordan & Bollman, 1890; *R.* "Amphi-American Assemblage" *texana* Chandler, 1921; *R.* "Amphi-American Assemblage" *cervigoni* Bigelow & Schroeder, 1964; *R.* "Amphi-American Assemblage" *bahamensis* Bigelow & Schroeder, 1965; and *R.* "Amphi-American Assemblage" *velezi* Chirichigno, 1973. Molecular analyses (Yang *et al*., unpubl.) indicate that two of these species, *R. eglanteria* and *R. velezi* (no data for the other taxa), group with another of McEachran & Dunn's (1998) rajine taxa, *Rostroraja* (i.e. *Rostroraja alba* (Lacepède, 1803)), within the newly erected tribe Rostrorajini (Chiquillo *et al*., 2014). Hence, retention of *Raja* (in the Rajini) for this group is untenable so the *Raja* "Amphi-American Assemblage" is provisionally assigned to *Rostroraja* following the recommendation of Naylor *et al*. (2012a,b). Nevertheless, *Rostroraja alba* differs morphologically from members of the *Raja* "Amphi-American Assemblage" and is a massive skate occurring in the Eastern Atlantic and South-West Indian Ocean (rather than the Western Atlantic and Eastern Pacific). More research is needed to verify this placement.

Reassignment of species to the genus *Dentiraja Whitley*, 1940

The genus *Dentiraja* was originally described as a subgenus of *Raja* Linnaeus by Whitley (1940), with *Raja dentata* Klunzinger, 1872 as type species. The species was later found to be a junior synonym of *Raia lemprieri* Richardson, 1845 (Paxton *et al*., 1989; Gomon *et al*., 1994; Last & Stevens, 1994; Hoese *et al*., 2006), which has subsequently been referred to as *Raja lemprieri* (Paxton *et al*., 1989; Gomon *et al*., 1994), *Raja* (*Dipturus*) *lemprieri* (Last & Stevens, 1994), *Dipturus lemprieri* (Last & Yearsley, 2002; Hoese *et al*., 2006; Jeong *et al*., 2007) and *Okamejei lemprieri* (McEachran & Dunn, 1998; Compagno, 1999; Ebert & Compagno, 2007).

The subgenus *Dentiraja* was resurrected and assigned to *Dipturus* Rafinesque, 1810 by Last & Yearsley (2002). Last & Gledhill (2008) subsequently elevated *Dentiraja* to full generic rank, based particularly on clasper morphology.

Recently, all species of the family Rajidae have been reviewed for the rajid chapter (Last *et al*., in press c) in the *Rays of the World* (Last *et al*., in press a). As pointed out in the remarks column of Table II for the respective species in Weigmann (2016), unpublished molecular results by Naylor (pers. comm.) indicated that several further species of *Dipturus* in fact belong to *Dentiraja*, i.e. *Dipturus australis* (Macleay, 1884), *Dipturus cerva* (Whitley, 1939), *Dipturus confusus* Last, 2008, *Dipturus endeavouri* Last, 2008 and *Dipturus polyommata* (Ogilby, 1910). Further data collected for the *Rays of the World* indicate that *Dipturus falloargus* Last, 2008, *Dipturus healdi* Last, White & Pogonoski, 2008 and *Dipturus oculus* Last, 2008 belong to *Dentiraja* as well. Accordingly, *Dentiraja* now comprises 10 valid species, i.e. *Dentiraja australis* (Macleay, 1884), *Dentiraja cerva* (Whitley, 1939), *Dentiraja confusa* (Last, 2008), *Dentiraja endeavouri* (Last, 2008), *Dentiraja falloarga* (Last, 2008), *Dentiraja flindersi* Last & Gledhill, 2008, *Dentiraja healdi* (Last, White & Pogonoski, 2008), *Dentiraja lemprieri* (Richardson, 1845), *Dentiraja oculata* (Last, 2008) and *Dentiraja polyommata* (Ogilby, 1910).

Species of *Dentiraja* differ from *Dipturus* species in the small (*vs*. large) size, short to moderately elongate (*vs*. elongate to very elongate) snout, and large internarial width usually exceeding 60% of prenasal snout length in adults (*vs*. usually less than 60% in adults). *Dentiraja* species resemble species of *Okamejei* Ishiyama, 1958 in the small size, but differ in the short (*vs*. long) inter- and postdorsal tail sections, and the absence (*vs*. presence, except for *Okamejei ornata* Weigmann, Stehmann & Thiel, 2015) of an external clasper component funnel. For clasper details of *Okamejei ornata* see Weigmann *et al*. (2015).

Annotated checklist for the order Rajiformes

The order Rajiformes consists of at least 291 species in four families: 14 species belong to the family Anacanthobatidae, 104 to the Arhynchobatidae, 19 to the Gurgesiellidae, and 154 to the Rajidae. The checklist is annotated and ordered by tribes within families (Table 1, see page 18). Assignments are supported by a combination of a molecular analysis of the mitochondrial genome (Yang *et al*., unpubl.) and morphological data (Last, Séret & Weigmann, unpubl.). Molecular data provide support for the retention of the 5 tribes of McEachran & Dunn (1998): Amblyrajini, Gurgesiellini, Rajini, as well as the Rostrorajini (Chiquillo *et al*., 2014) in the subfamily Rajinae; and Aryhnchobatini and Riorajini in the Arhynchobatinae. There is also strong evidence for the resurrection of the Pavorajini McEachran, 1984 (modified generic composition) and inclusion of two taxa that are newly erected herein, Bathyrajini (type genus *Bathyraja* Ishiyama, 1958) and Crurirajini (type genus *Cruriraja* Bigelow & Schroeder, 1948).

The family Rajidae now comprises 3 tribes. The Amblyrajini (*sensu* McEachran & Dunn) contained 5 genera (*Amblyraja*, *Breviraja*, *Dactylobatus*, *Leucoraja* and *Rajella*). While no samples of *Dactylobatus* were available, there is strong support for the inclusion of the remaining taxa in this tribe of the Rajidae. The tribe Rajini (*sensu* McEachran & Dunn) of the subfamily Rajinae contained 8 genera (*Anacanthobatis*, *Cruriraja*, *Dipturus*, *Okamejei*, *Raja*, *Rostroraja*, and two un-named taxa). Based on molecular data (Yang *et al*., unpubl.), the tribe now contains *Dipturus*, *Okamejei*, and *Raja*, as well as 5 additional taxa, *Beringraja*, *Dentiraja*, *Hongeo*, *Spiniraja* and *Zearaja* (all supported by morphological and molecular data). *Dipturus intermedius* (Parnell, 1837) is resurrected from the synonymy of *D. batis* (Linnaeus, 1758) based on Iglésias *et al*. (2010). *Anacanthobatis* and *Cruriraja* are transferred to other families (i.e. Anacanthobatidae and Gurgesiellidae respectively), and *Rostroraja* is transferred to the Rostrorajini. The third tribe of the Rajidae, the Rostrorajini, includes four genera *Malacoraja*, *Neoraja*, *Orbiraja* and *Rostroraja*. *Malacoraja* and *Neoraja* were formerly assigned to the Gurgesiellini (in the Rajinae) by McEachran & Dunn.

The family Arhynchobatidae now comprises 4 tribes. The Arhynchobatini (*sensu* McEachran & Dunn) consisted of 9 genera (*Arhynchobatis*, *Bathyraja*, *Irolita*, *Notoraja*, *Psammobatis*, *Pavoraja*, *Pseudoraja*, *Rhinoraja* and *Sympterygia*). It is now divided to include only the 4 genera *Arhynchobatis*, *Irolita*, *Psammobatis* and *Sympterygia* (all supported by molecular data). The Riorajini (*sensu* McEachran & Dunn) contained *Atlantoraja* and *Rioraja* and this association is well supported. An Indo–Pacific group defined by McEachran (1984) as the Pavorajini is resurrected herein and contains *Brochiraja*, *Insentiraja*, *Notoraja* and *Pavoraja* with very strong molecular support. *Pseudoraja* is provisionally retained in this group, but most likely will be assigned to the family Gurgesiellidae when fresh material is made available for study. *Bathyraja* and *Rhinoraja* are assigned to a newly erected tribe, the Bathyrajini.

The family Gurgesiellidae contains 2 strongly divergent groups based on both molecular and morphological data. The Gurgesiellini contains a single genus (*Gurgesiella*) and 3 species. A newly erected tribe Crurirajini contains *Cruriraja* (assigned to the Rajini by McEachran & Dunn) and *Fenestraja* (assigned to the Gurgesiellini of the subfamily Rajinae by McEachran & Dunn).

Anacanthobatis was assigned to the Rajini (Rajinae) by McEachran & Dunn. The family Anacanthobatidae now includes *Anacanthobatis* and species reassigned to 4 other genera (*Indobatis*, *Schroederobatis*, *Sinobatis* and *Springeria*) based on recent morphological research (Hulley, 1973; Weigmann *et al*., 2014a; Stehmann & Weigmann, 2016).

Some nominal species included (except for *Raja arctowskii*) as questionable species in Weigmann (2016) could not be definitely assigned to valid taxa. Therefore, the following species are provisionally considered invalid and need further evaluation:

- *Raja alia* Garman, 1899 is considered a *nomen dubium* (Weigmann, 2016) and may be a junior synonym of *Rostroraja ackleyi* (Garman, 1881).
- *Raja arctowskii* Dollo, 1904, based on empty egg capsules, is probably valid and possibly identical to *Bathyraja* sp. 2 *sensu* Stehmann (1985) following Weigmann (2016).
- *Raja rondeleti* Bougis, 1959 is questionably valid (Weigmann, 2016). Considered doubtful according to Compagno (1999, 2005), but valid following Capapé *et al*. (2006). Probably synonymous with either *Raja clavata* (Stehmann & Bürkel, 1984) or *Leucoraja fullonica* (Serena, 2005). See Weigmann (2016) for more information.
- *Anacanthobatis donghaiensis* (Deng, Xiong & Zhan, 1983) is a likely junior synonym of *Sinobatis borneensis* (Séret, 1986). See Weigmann (2016) for more information.
- *Anacanthobatis nanhaiensis* (Meng & Li in Chu *et al*., 1981) is a likely junior synonym of *Sinobatis borneensis* (Ishihara, 1984; Last & Compagno, 1999; Last & Séret, 2008; White & Last, 2013). See Weigmann (2016) for more information.

Table 1. Annotated checklist for the order Rajiformes

Rajidae

Amblyrajini

Amblyraja doellojuradoi (Pozzi, 1935)
Amblyraja frerichsi (Krefft, 1968) Possibly a junior synonym of *A. hyperborea* due to strong morphological similarity according to Ebert & Stehmann (2013) and Weigmann (2016).
Amblyraja georgiana (Norman, 1938) Morphologically distinct but confused with *A. hyperborea* leading to possible misidentification of preliminary molecular data (Last, unpubl.).
Amblyraja hyperborea (Collett, 1879) *Raja badia* Garman, 1899 and *Raja robertsi* Hulley, 1970 are considered synonyms (Weigmann, 2016; Last, unpubl.). The literature also contains examples of several valid *Amblyraja* that have been confused with this species.
Amblyraja jenseni (Bigelow & Schroeder, 1950) Provisionally retained but treated as junior synonym of *A. hyperborea* by Weigmann (2016) due to strong morphological similarity and preliminary molecular data. Further work is needed to resolve this issue.
Amblyraja radiata (Donovan, 1808)
Amblyraja reversa (Lloyd, 1906) Retained in *Amblyraja* but generic placement questionable (Last, unpubl.) and needs further investigation.
Amblyraja taaf (Meisner, 1987) Possibly a junior synonym of *A. hyperborea* due to strong morphological similarity according to Ebert & Stehmann (2013) and Weigmann (2016).
Breviraja claramaculata McEachran & Matheson, 1985
Breviraja colesi Bigelow & Schroeder, 1948
Breviraja mouldi McEachran & Matheson, 1995
Breviraja nigriventralis McEachran & Matheson, 1985
Breviraja spinosa Bigelow & Schroeder, 1950
Dactylobatus armatus Bean & Weed, 1909 Placement of *Dactylobatus* not yet assed for molecular data.
Dactylobatus clarkii (Bigelow & Schroeder, 1958)
Leucoraja circularis (Couch, 1838)
Leucoraja compagnoi (Stehmann, 1995)
Leucoraja erinacea (Mitchell, 1825)
Leucoraja fullonica (Linnaeus, 1758)
Leucoraja garmani (Whitley, 1939) *Leucoraja garmani* contains two valid subspecies: *Leucoraja garmani caribbaea* (McEachran, 1977) and *Leucoraja garmani virginica* (McEachran, 1977) (Schmitter-Soto *et al*., 2000; McEachran 2002; Moore *et al*., 2003; Weigmann, 2016).
Leucoraja lentiginosa (Bigelow & Schroeder, 1951)
Leucoraja leucosticta (Stehmann, 1971)
Leucoraja melitensis (Clark, 1926)

Leucoraja naevus (Müller & Henle, 1841)
Leucoraja ocellata (Mitchill, 1815)
Leucoraja pristispina Last, Stehmann & Séret, 2008
Leucoraja wallacei (Hulley, 1970)
Leucoraja yucatanensis (Bigelow & Schroeder, 1950)
Rajella annandalei (Weber, 1913)
Rajella barnardi (Norman, 1935)
Rajella bathyphila (Holt & Byrne, 1908)
Rajella bigelowi (Stehmann, 1978)
Rajella caudaspinosa (von Bonde & Swart, 1923)
Rajella challengeri Last & Stehmann, 2008
Rajella dissimilis (Hulley, 1970)
Rajella eisenhardti Long & McCosker, 1999 Not included in Compagno (2005).
Rajella fuliginea (Bigelow & Schroeder, 1954)
Rajella fyllae (Lütken, 1887) *Breviraja marklei* McEachran & Miyake, 1987 is a junior synonym (Stehmann *et al*., 2008; Weigmann, 2016).
Rajella kukujevi (Dolganov, 1985)
Rajella leoparda (von Bonde & Swart, 1923) Formerly as *R. leopardus* but amended to *R. leoparda* in accordance with ICZN Article 34.2. by Weigmann *et al*. (2014b). Still spelt *R. leopardus* by Compagno (2005).
Rajella lintea (Fries, 1838) Generally listed as published in 1838 (Eschmeyer *et al*., 2016), but as 1839 in Stehmann (2012) and Weigmann (2016). As *Dipturus*? *linteus* by Compagno (2005).
Rajella nigerrima (de Buen, 1960)
Rajella paucispinosa Weigmann, Stehmann & Thiel, 2014
Rajella purpuriventralis (Bigelow & Schroeder, 1962) Placed erroneously in *Dipturus* Rafinesque, 1810 based on material from the Gulf of Mexico (Weigmann, 2016) following Cotton & Stehmann (pers. comm), but this was based on a misidentification.
Rajella ravidula (Hulley, 1970)
Rajella sadowskii (Krefft & Stehmann, 1974) Spelt *R. sadowskyii* by Compagno (2005).

Rajini

Beringraja binoculata (Girard, 1855) Initially placed in *Beringraja* Ishihara, Treloar, Bor, Senou & Jeong, 2012 by Ishihara *et al*. (2012) with very strong molecular support (Yang *et al*., unpubl.).
Beringraja cortezensis (McEachran & Miyake, 1988) Newly assigned to *Beringraja* with strong molecular support (Yang *et al*., unpubl.).
Beringraja inornata (Jordan & Gilbert, 1881) Newly assigned to *Beringraja* with strong molecular support (Yang *et al*., unpubl.).
Beringraja pulchra (Liu, 1932) Type of *Beringraja*. As *Raja 'pulchra'*, junior homonym of *Raja pulchra* Schafhaeutl, 1863 for fossil dermal tubercles from the Eocene of Bavaria by Compagno (2005).
Beringraja rhina (Jordan & Gilbert, 1880) Newly assigned to *Beringraja* with strong molecular support (Yang *et al*., unpubl.).
Beringraja stellulata (Jordan & Gilbert, 1880) Newly assigned to *Beringraja* with strong molecular support (Yang *et al*., unpubl.).
Dentiraja australis (Macleay, 1884) Recently placed in *Dipturus* by Last & Stevens (2009) and Weigmann (2016) but now assigned to *Dentiraja* Whitley, 1940 following new molecular data (Yang *et al*., unpubl.). As *Okamejei australis* by Compagno (2005).
Dentiraja cerva (Whitley, 1939) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.). As *Okamejei cerva* by Compagno (2005).
Dentiraja confusa (Last, 2008) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.).
Dentiraja endeavouri (Last, 2008) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.).
Dentiraja falloarga (Last, 2008) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.).
Dentiraja flindersi Last & Gledhill, 2008 Reassigned from *Dipturus* to *Dentiraja* by Last & Gledhill (2008).
Dentiraja healdi (Last, White & Pogonoski, 2008) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.).
Dentiraja lemprieri (Richardson, 1845) Reassigned from *Dipturus* to *Dentiraja* by Last & Gledhill (2008). As *Okamejei lemprieri* by Compagno (2005).
Dentiraja oculata (Last, 2008) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.).
Dentiraja polyommata (Ogilby, 1910) Newly assigned to *Dentiraja* based on molecular data (Yang *et al*., unpubl.). As *Raja polyommata* by Compagno (2005).
Dipturus acrobelus Last, White & Pogonoski, 2008
Dipturus amphispinus Last & Alava, 2013
Dipturus apricus Last, White & Pogonoski, 2008
Dipturus batis (Linnaeus, 1758) Still treated as a composite species in Weigmann (2016) but with remark that *D. batis* comprises a small (*D*. cf. *flossada*) and a large (*D*. cf. *intermedia*) species following Iglésias *et al*. (2010). As a single species, *D. batis,* by Compagno (2005) and used herein for (*D*. cf. *flossada).*

Dipturus bullisi (Bigelow & Schroeder, 1962)
Dipturus campbelli (Wallace, 1967)
Dipturus canutus Last, 2008 Molecular data (Yang *et al*., unpubl.) supports placement in *Dipturus* rather than *Dentiraja*.
Dipturus chinensis (Basilewsky, 1855) Considered valid by Cheng & Zhou (1997) in the genus *Raja* but questionably valid by Weigmann (2016). New data confirm its validity and indicate its assignment to *Dipturus* (Last, unpubl.). Not included in Compagno (2005).
Dipturus crosnieri (Séret, 1989)
Dipturus doutrei (Cadenat, 1960)
Dipturus ecuadoriensis (Beebe & Tee-Van, 1941)
Dipturus garricki (Bigelow & Schroeder, 1958)
Dipturus gigas (Ishiyama, 1958)
Dipturus grahami Last, 2008
Dipturus gudgeri (Whitley, 1940) As *Dipturus*? *gudgeri* by Compagno (2005).
Dipturus innominatus (Garrick & Paul, 1974) As *Dipturus*? *innominatus* by Compagno (2005).
Dipturus intermedius (Parnell, 1837) Newly resurrected from the synonymy of *Dipturus batis* (Linnaeus, 1758) based on Iglésias *et al*. (2010). Not in Compagno (2005) and still treated as a composite species in *D. batis* by Weigmann (2016).
Dipturus johannisdavisi (Alcock, 1899) Spelt *D. johannisdavesi* by Compagno (2005).
Dipturus kwangtungensis (Chu, 1960) Confused with *Dipturus chinensis* (Basilewsky, 1855) in recent literature.
Dipturus laevis (Mitchill, 1818)
Dipturus lanceorostratus (Wallace, 1967) Spelt *D. lanceorostrata* by Compagno (2005).
Dipturus leptocaudus (Krefft & Stehmann, 1975) Spelt *D. leptocauda* by Compagno (2005).
Dipturus macrocaudus (Ishiyama, 1955) Spelt *D. macrocauda* by Compagno (2005).
Dipturus melanospilus Last, White & Pogonoski, 2008
Dipturus mennii Gomes & Paragó, 2001 *Dipturus diehli* Soto & Mincarone 2001 is a junior synonym of *D. mennii* (Moreira *et al*., 2011; Weigmann, 2016).
Dipturus nidarosiensis (Storm, 1881) Probably a composite species in the eastern North Atlantic according to Ebert & Stehmann (2013) and Weigmann (2016). However, at least one form appears widespread with populations from Ireland and South Africa identical based on molecular data (Yang *et al*., unpubl.). Authorship indicated as (Collett, 1880) by Compagno (2005).
Dipturus olseni (Bigelow & Schroeder, 1951)
Dipturus oregoni (Bigelow & Schroeder, 1958)

Dipturus oxyrinchus (Linnaeus, 1758) Probably a composite species comprising a small and a large species according to Ebert & Stehmann (2013) and Weigmann (2016). Spelt *D. oxyrhynchus* by Compagno (2005).
Dipturus pullopunctatus (Smith, 1964) Spelt *D. pullopunctata* by Compagno (2005).
Dipturus queenslandicus Last, White & Pogonoski, 2008
Dipturus springeri (Wallace, 1967)
Dipturus stenorhynchus (Wallace, 1967)
Dipturus teevani (Bigelow & Schroeder, 1951)
Dipturus tengu (Jordan & Fowler, 1903)
Dipturus trachydermus (Krefft & Stehmann, 1974) Spelt *D. trachyderma* by Compagno (2005).
Dipturus wengi Séret & Last, 2008
Dipturus wuhanlingi Jeong & Nakabo, 2008
Hongeo koreana (Jeong & Nakabo, 1997) Distinct morphologically and based on molecular data (Yang *et al*., unpubl.) from other rajine skates. As *Okamejei*? *koreana* by Compagno (2005).
Okamejei acutispina (Ishiyama, 1958)
Okamejei arafurensis Last & Gledhill, 2008
Okamejei boesemani (Ishihara, 1987)
Okamejei cairae Last, Fahmi & Ishihara, 2010
Okamejei heemstrai (McEachran & Fechhelm, 1982)
Okamejei hollandi (Jordan & Richardson, 1909)
Okamejei kenojei (Müller & Henle, 1841)
Okamejei leptoura Last & Gledhill, 2008
Okamejei meerdervoortii (Bleeker, 1860)
Okamejei mengae Jeong, Nakabo & Wu, 2007 Possibly a junior synonym of *O. hollandi* (Weigmann, 2016).
Okamejei ornata Weigmann, Stehmann & Thiel, 2015
Okamejei schmidti (Ishiyama, 1958)
Raja africana Capapé, 1977 Listed as valid by McEachran & Séret (2016) but questionable following Weigmann (2016) with the holotype supposedly representing an aberrant *R. miraletus* or *R. straeleni*, and a homonym, preoccupied by *Raja africana* Bloch & Schneider, 1801, which is now considered a junior synonym of a dasyatid *Urogymnus asperrimus*. Also treated as a questionably valid species by Compagno (2005).
Raja asterias Delaroche, 1809
Raja brachyura Lafont, 1873
Raja clavata Linnaeus, 1758
Raja herwigi Krefft, 1965

Raja maderensis Lowe, 1838 Recent molecular results indicate that *R. maderensis* is possibly conspecific with *R. clavata* (Ball *et al*., 2016).
Raja microocellata Montagu, 1818
Raja miraletus Linnaeus, 1758 Confused with *Raja ocellifera* Regan, 1906 and *Raja parva* Last & Séret, 2016 by McEachran & Séret 2016 and others (Last & Séret 2016).
Raja montagui Fowler, 1910
Raja ocellifera Regan, 1906 Frequently confused with *Raja miraletus* Linnaeus, 1758 but newly resurrected as a valid species by Last & Séret (2016).
Raja parva Last & Séret, 2016 Newly described species frequently confused with *Raja miraletus*.
Raja pita Fricke & Al-Hassan, 1995 Placed as *incertae sedis* in the general genus *Raja*, probably belonging to either *Leucoraja* Malm 1877 or *Rajella* Stehmann 1970 (Weigmann *et al*., 2015; Weigmann, 2016). As *Okamejei pita* by Compagno (2005).
Raja polystigma Regan, 1923
Raja radula Delaroche, 1809
Raja straeleni Poll, 1951
Raja undulata Lacepède, 1802
Spiniraja whitleyi (Iredale, 1938) Support for this genus-level taxon based on Last (unpubl.) and Yang *et al*. (unpubl.).
Zearaja argentinensis (de Astarloa, Mabragana, Hanner & Figueroa, 2008) Placed in *Zearaja* Whitley, 1939 instead of *Dipturus* Rafinesque, 1810, based on Yang *et al*. (unpubl.); see also Weigmann (2016).
Zearaja chilensis (Guichenot, 1848) Possibly a composite species based on molecular analyses (Naylor *et al*., 2012b; Vargas-Caro *et al*., 2014; Weigmann, 2016). As *Dipturus*? *chilensis* by Compagno (2005).
Zearaja maugeana Last & Gledhill, 2007
Zearaja nasuta (Müller & Henle, 1841) As *Dipturus*? *nasutus* by Compagno (2005).

Rostrorajini

Malacoraja kreffti (Stehmann, 1978)
Malacoraja obscura Carvalho, Gomes & Gadig, 2005
Malacoraja senta (Garman, 1885)
Malacoraja spinacidermis (Barnard, 1923)
Neoraja africana (Stehmann & Séret, 1983)
Neoraja caerulea (Stehmann, 1976)
Neoraja carolinensis McEachran & Stehmann, 1984
Neoraja iberica Stehmann, Séret, Costa & Baro, 2008 Morphologically distinct from *Neoraja caerulea* (Stehmann, 1976) but the species are indistinguishable based on their *NADH2 gene sequences* (Yang *et al*., unpubl.).

Neoraja stehmanni (Hulley, 1972)
Orbiraja jensenae (Last & Lim, 2010) Relocated to newly described genus *Orbiraja* Last, Weigmann & Dumale, 2016 (Last *et al*., 2016).
Orbiraja philipi (Lloyd, 1906) Now placed in *Orbiraja* (Last *et al*., 2016) *but* possibly a junior synonym of *O. powelli* (Weigmann *et al*., 2015; Weigmann, 2016).
Orbiraja powelli (Alcock, 1898) Now placed in *Orbiraja* (Last *et al*., 2016).
Rostroraja ackleyi (Garman, 1881) Provisionally assigned to *Rostroraja* based on molecular data (Yang *et al*., unpubl). Placed as *incertae sedis* in the general genus *Raja* by Compagno (2005) and Weigmann (2016).
Rostroraja alba (Lacepède 1803)
Rostroraja bahamensis (Bigelow & Schroeder, 1965) Provisionally assigned to *Rostroraja* based on molecular data (Yang *et al*., unpubl). Placed as *incertae sedis* in the general genus *Raja* by Compagno (2005) and Weigmann (2016).
Rostroraja cervigoni (Bigelow & Schroeder, 1964) See comment above for *Rostroraja bahamensis*.
Rostroraja eglanteria (Bosc, 1800) See comment above for *Rostroraja bahamensis*.
Rostroraja equatorialis (Jordan & Bollman, 1890) See comment above for *Rostroraja bahamensis*.
Rostroraja texana (Chandler, 1921) See comment above for *Rostroraja bahamensis*.
Rostroraja velezi (Chirichigno, 1973) See comment above for *Rostroraja bahamensis*.

Arhynchobatidae

Arhynchobatini

Arhynchobatis asperrimus Waite, 1909
Irolita waitii (McCulloch, 1911) Spelt *I. waitei* by Compagno (2005).
Irolita westraliensis Last & Gledhill, 2008
Psammobatis bergi Marini, 1932
Psammobatis extenta (Garman, 1913)
Psammobatis lentiginosa McEachran, 1983
Psammobatis normani McEachran, 1983
Psammobatis parvacauda McEachran, 1983 Unpublished data support the validity of this rare species (Weigmann, 2016).
Psammobatis rudis Günther, 1870
Psammobatis rutrum Jordan, 1891
Psammobatis scobina (Philippi, 1857)

Sympterygia acuta Garman, 1877
Sympterygia bonapartii Müller & Henle, 1841 Spelt *S. bonapartei* by Compagno (2005).
Sympterygia brevicaudata (Cope, 1877)
Sympterygia lima (Poeppig, 1835)

Bathyrajini

Bathyraja abyssicola (Gilbert, 1896)
Bathyraja aguja (Kendall & Radcliffe, 1912)
Bathyraja albomaculata (Norman, 1937) Compagno (1999) reallocated this species from *Bathyraja* Ishiyama, 1958 to *Rhinoraja* Ishiyama, 1952, but the validity of this move is questionable (Weigmann, 2016; Last, unpubl.).
Bathyraja aleutica (Gilbert, 1896)
Bathyraja andriashevi Dolganov, 1983
Bathyraja bergi Dolganov, 1983
Bathyraja brachyurops (Fowler, 1910) Probably belongs to the subgenus *Arctoraja* Ishiyama, 1958 based on clasper characters (Stehmann, pers. comm. in Weigmann, 2016).
Bathyraja cousseauae Diaz de Astarloa & Mabragana, 2004 Spelt *B. cousseaui* by Compagno (2005).
Bathyraja diplotaenia (Ishiyama, 1952)
Bathyraja eatonii (Günther, 1876)
Bathyraja fedorovi Dolganov, 1983
Bathyraja griseocauda (Norman, 1937)
Bathyraja hesperafricana Stehmann, 1995
Bathyraja interrupta (Gill & Townsend, 1897) Following Weigmann (2016), as *Rhinoraja interrupta* by Raschi & McEachran (1991), Compagno (1999, 2005), Dolganov (1999), Sheiko & Fedorov (2000), Hoff (2002) and Orlov (2003), but as *Bathyraja interrupta* by Stehmann (1986), McEachran & Dunn (1998), Mecklenburg *et al*. (2002), Spies *et al*. (2011) and Page *et al*. (2013). Spies *et al*. (2011) provide morphological and molecular support for the placement in *Bathyraja* instead of *Rhinoraja*. *Bathyraja interrupta* possibly represents a species complex (Orr *et al*., 2011; Spies *et al*., 2011; Weigmann, 2016).
Bathyraja irrasa Hureau & Ozouf-Costaz, 1980
Bathyraja ishiharai Stehmann, 2005
Bathyraja isotrachys (Günther, 1877)
Bathyraja kincaidii (Garman, 1908) Treated as junior synonym of *B. interrupta* by Weigmann (2016) following Ishihara & Ishiyama (1985), Stehmann (1986), Sheiko & Fedorov (2000) and Ishihara (pers. comm.), but as valid species spelt *B. kincaidi* by Compagno (2005). Further work is needed to resolve this issue.
Bathyraja leucomelanos Iglésias & Lévy-Hartmann, 2012
Bathyraja lindbergi Ishiyama & Ishihara, 1977 Valid according to Compagno (1999, 2005), Weigmann (2016) and Last (unpubl.), but a junior synonym of *B. matsubarai* according to Sheiko & Fedorov (2000).

Bathyraja longicauda (de Buen, 1959)
Bathyraja maccaini Springer, 1971
Bathyraja macloviana (Norman, 1937) Compagno (1999) reallocated this species from *Bathyraja* to *Rhinoraja*, but the validity of this move is questionable (Weigmann, 2016; Last, unpubl.).
Bathyraja maculata Ishiyama & Ishihara, 1977
Bathyraja magellanica (Philippi, 1902) Compagno (1999) reallocated this species from *Bathyraja* to *Rhinoraja*, but the validity of this move is questionable (Weigmann, 2016; Last, unpubl.).
Bathyraja mariposa Stevenson, Orr, Hoff & McEachran, 2004
Bathyraja matsubarai (Ishiyama, 1952) *Bathyraja caeluronigricans* Ishiyama & Ishihara, 1977 is a junior synonym (Ishihara, 1990; Weigmann, 2016; Last, unpubl.).
Bathyraja meridionalis Stehmann, 1987
Bathyraja microtrachys (Osburn & Nichols, 1916) Treated as junior synonym of *B. trachura* by Weigmann (2016) following Castro-Aguirre & Espinosa Pérez (1996) and Mecklenburg *et al*. (2002), but as valid species by Compagno (2005). Further work is needed to resolve this issue.
Bathyraja minispinosa Ishiyama & Ishihara, 1977
Bathyraja multispinis (Norman, 1937) Compagno (1999) reallocated this species from *Bathyraja* to *Rhinoraja*, but the validity of this move is questionable (Weigmann, 2016; Last, unpubl.).
Bathyraja murrayi (Günther, 1880) Compagno (1999) reallocated this species from *Bathyraja* to *Rhinoraja*, but the validity of this move is questionable (Weigmann, 2016; Last, unpubl.).
Bathyraja notoroensis Ishiyama & Ishihara, 1977 Treated as junior synonym of *B. matsubarai* by Weigmann (2016) following Ishihara (1990), but as valid species by Compagno (2005). Further work is needed to resolve this issue (Last, unpubl.).
Bathyraja pacifica Last, Stewart & Séret, 2016 Newly described species.
Bathyraja pallida (Forster, 1967)
Bathyraja panthera Orr, Stevenson, Hoff, Spies & McEachran, 2011 Belongs to the subgenus *Arctoraja* (Orr *et al*., 2011; Weigmann, 2016).
Bathyraja papilionifera Stehmann, 1985
Bathyraja parmifera (Bean, 1881) Belongs to the subgenus *Arctoraja* (Orr *et al*., 2011; Weigmann, 2016). *Rhinoraja obtusa* (Gill & Townsend, 1897) and *Rhinoraja rosispinis* (Gill & Townsend, 1897) are junior synonyms (Stehmann 1986; Mecklenburg *et al*., 2002; Orr *et al*., 2011; Weigmann, 2016).
Bathyraja peruana McEachran & Miyake, 1984
Bathyraja richardsoni (Garrick, 1961)
Bathyraja scaphiops (Norman, 1937)
Bathyraja schroederi (Krefft, 1968)
Bathyraja shuntovi Dolganov, 1985

Bathyraja simoterus (Ishiyama, 1967) Belongs to the subgenus *Arctoraja* (Orr *et al*., 2011; Weigmann, 2016). According to Weigmann (2016), a junior synonym of *B. parmifera* following Dolganov (2001) and Dolganov & Korolev (2006), but valid according to Stehmann (1986), McEachran & Dunn (1998), Compagno (1999, 2005), Nakabo (2002, 2013), Orr *et al*. (2011) and Spies *et al*. (2011).
Bathyraja smirnovi (Soldatov & Pavlenko, 1915) See comment above for *Bathyraja simoterus*.
Bathyraja smithii (Müller & Henle, 1841)
Bathyraja spinicauda (Jensen, 1914)
Bathyraja spinosissima (Beebe & Tee-Van, 1941)
Bathyraja taranetzi (Dolganov, 1983) As *Rhinoraja taranetzi* by Weigmann (2016). Following Weigmann (2016), as *Bathyraja taranetzi* by Mecklenburg *et al*. (2002) and Page *et al*. (2013), but as *Rhinoraja taranetzi* by Raschi & McEachran (1991), McEachran & Dunn (1998), Compagno (1999, 2005), Dolganov (1999), Sheiko & Fedorov (2000), Stevenson *et al*. (2004), Spies *et al*. (2011) and Ishihara (pers. comm.). *Rhinoraja longi* Raschi & McEachran, 1991 is a junior synonym (Mecklenburg *et al*., 2002; Stevenson *et al*., 2004; Weigmann, 2016).
Bathyraja trachouros (Ishiyama, 1958)
Bathyraja trachura (Gilbert, 1892)
Bathyraja tunae Stehmann, 2005 Possibly conspecific with the wide-ranging *Bathyraja richardsoni* (Garrick, 1961) (Last, unpubl.).
Bathyraja tzinovskii Dolganov, 1983
Bathyraja violacea (Suvorov, 1935)
Rhinoraja kujiensis (Tanaka, 1916) *Bathyraja* and *Rhinoraja* were considered among the most problematic of the chondrichthyan genera by Naylor *et al*. (2012a). All species assigned to *Rhinoraja* were found to be interspersed among the 20 species of *Bathyraja* included in their molecular analysis. However, none of the species originally assigned to *Rhinoraja* by Ishiyama (1952, 58) was included. The separation of *Rhinoraja* from *Bathyraja* is still doubtful as the only diagnostic character is the presence or absence of a segmented rostral cartilage (Ishihara, pers. comm. in Weigmann, 2016). For the time being, *Rhinoraja* is retained pending further investigation.
Rhinoraja longicauda Ishiyama, 1952 See comment above.
Rhinoraja odai Ishiyama, 1958 See comment above.

Riorajini

Atlantoraja castelnaui (Miranda Ribeiro, 1907) Author name indicated as Ribeiro by Compagno (2005).
Atlantoraja cyclophora (Regan, 1903)
Atlantoraja platana (Günther, 1880)
Rioraja agassizii (Müller & Henle, 1841)

Pavorajini

Brochiraja aenigma Last & McEachran, 2006
Brochiraja albilabiata Last & McEachran, 2006
Brochiraja asperula (Garrick & Paul, 1974) Still as *Notoraja asperula* by Compagno (2005).
Brochiraja heuresa Last & Séret, 2012
Brochiraja leviveneta Last & McEachran, 2006
Brochiraja microspinifera Last & McEachran, 2006
Brochiraja spinifera (Garrick & Paul, 1974) Still as *Notoraja spinifera* by Compagno (2005).
Brochiraja vittacauda Last & Séret, 2012
Insentiraja laxipella Yearsley & Last, 1992 As *Notoraja laxipella* by Compagno (2005). Status of *Insentiraja* needs further investigation (Last, unpubl.).
Insentiraja subtilispinosa (Stehmann, 1989) As *Notoraja subtilispinosa* with date of the original publication given as 1985 by Compagno (2005).
Notoraja alisae Séret & Last, 2012
Notoraja azurea McEachran & Last, 2008
Notoraja fijiensis Séret & Last, 2012
Notoraja hirticauda Last & McEachran, 2006
Notoraja inusitata Séret & Last, 2012
Notoraja lira McEachran & Last, 2008
Notoraja longiventralis Séret & Last, 2012
Notoraja ochroderma McEachran & Last, 1994
Notoraja sapphira Séret & Last, 2009
Notoraja sticta McEachran & Last, 2008
Notoraja tobitukai (Hiyama, 1940)
Pavoraja alleni McEachran & Fechhelm, 1982
Pavoraja arenaria Last, Mallick & Yearsley, 2008
Pavoraja mosaica Last, Mallick & Yearsley, 2008
Pavoraja nitida (Günther, 1880)
Pavoraja pseudonitida Last, Mallick & Yearsley, 2008
Pavoraja umbrosa Last, Mallick & Yearsley, 2008
?*Pseudoraja fischeri* Bigelow & Schroeder, 1954

Gurgesiellidae

Cruririajini

Cruriraja andamanica (Lloyd, 1909)
Cruriraja atlantis Bigelow & Schroeder, 1948
Cruriraja cadenati Bigelow & Schroeder, 1962
Cruriraja durbanensis (von Bonde & Swart, 1923)
Cruriraja hulleyi Aschliman, Ebert & Compagno, 2010
Cruriraja parcomaculata (von Bonde & Swart, 1923) *Cruriraja triangularis* Smith, 1964 is a junior synonym (Compagno & Ebert, 2007; Aschliman *et al*., 2010; Weigmann, 2016).
Cruriraja poeyi Bigelow & Schroeder, 1948
Cruriraja rugosa Bigelow & Schroeder, 1958
Fenestraja atripinna (Bigelow & Schroeder, 1950)
Fenestraja cubensis (Bigelow & Schroeder, 1950)
Fenestraja ishiyamai (Bigelow & Schroeder, 1962)
Fenestraja maceachrani (Séret, 1989)
Fenestraja mamillidens (Alcock, 1889)
Fenestraja plutonia (Garman, 1881)
Fenestraja sibogae (Weber, 1913)
Fenestraja sinusmexicanus (Bigelow & Schroeder, 1950)

Gurgesiellini

Gurgesiella atlantica (Bigelow & Schroeder, 1962)
Gurgesiella dorsalifera McEachran & Compagno, 1980
Gurgesiella furvescens de Buen, 1959

Anacanthobatidae

Anacanthobatini

Anacanthobatis marmorata (von Bonde & Swart, 1923) Formerly as *A. marmoratus* but amended to *A. marmorata* in accordance with ICZN Article 34.2. by Weigmann *et al*. (2014a). Date of the original description indicated as 1924 by Compagno (2005).
Indobatis ori (Wallace, 1967) Still placed in *Anacanthobatis* by Compagno (2005).
Schroederobatis americana (Bigelow & Schroeder, 1962) As *Anacanthobatis americanus* by Compagno (2005). Still placed in the subgenus *Schroederobatis* Hulley, 1973 of genus *Anacanthobatis* von Bonde & Swart, 1923 by Weigmann *et al*. (2014a), Weigmann (2016), Weigmann & Stehmann (2016) and Stehmann & Weigmann (2016). Specific name amended from *americanus* to *americana* in accordance with ICZN Article 34.2. by Weigmann *et al*. (2014a).
Sinobatis andamanensis Last & Bussarawit, 2016 Newly described species.
Sinobatis borneensis (Chan, 1965) As *Anacanthobatis borneensis* by Compagno (2005), but assigned to *Sinobatis* by Last & Séret (2008).

Sinobatis brevicauda Weigmann & Stehmann, 2016 Newly described species.
Sinobatis bulbicauda Last & Séret, 2008
Sinobatis caerulea Last & Séret, 2008
Sinobatis filicauda Last & Séret, 2008
Sinobatis kotlyari Stehmann & Weigmann, 2016 Newly described species, not included in the *Rays of the World* family contribution Anacanthobatidae (Séret *et al*., in press).
Sinobatis melanosoma (Chan, 1965) As *Anacanthobatis melanosoma* by Compagno (2005), but provisionally assigned to *Sinobatis* by Last & Séret (2008), which was supported by the examination of the claspers of a subadult male by Weigmann *et al*. (2014a).
Sinobatis stenosoma (Li & Hu, in Chu, Meng, Hu & Li, 1982) As *Anacanthobatis stenosoma* by Compagno (2005). As questionably valid species in the general genus *Anacanthobatis* by Weigmann (2016) based on Ishihara & Ishiyama (1986), Séret (1986), and Last & Compagno (1999), who treated the species as possibly invalid, and White & Last (2013), who treated it as questionably valid.
Springeria folirostris Bigelow & Schroeder, 1951 As *Anacanthobatis folirostris* by Compagno (2005). Still placed in the subgenus *Springeria* Bigelow & Schroeder, 1951 of genus *Anacanthobatis* by Weigmann *et al*. (2014a), Weigmann (2016), Weigmann & Stehmann (2016) and Stehmann & Weigmann (2016).
Springeria longirostris (Bigelow & Schroeder, 1962) As *Anacanthobatis longirostris* by Compagno (2005). Still placed in the subgenus *Springeria* of genus *Anacanthobatis* by Weigmann *et al*. (2014a), Weigmann (2016), Weigmann & Stehmann (2016) and Stehmann & Weigmann (2016).

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