HAKES OF THE WORLD
(Family Merlucciidae)

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF HAKE SPECIES KNOWN TO DATE
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by

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The hake family Merlucciidae has been an important part of the fishing industry, as many of its species sustain a significant fishery. There is much existing literature on the biology and dynamics of its populations, however, the problem of species identification remains, owing to the difficulty of finding easily observable, stable characters that permit rigorous identification. These difficulties can become critical where species distributions overlap.

This document provides an identification key based on easily observable qualitative and meristic characters, which enable fast and precise diagnosis. Its objective is to make available to fishery professionals a reliable tool for species identification and thereby improve their gathering of statistical data. Given that many of the species are of great fishery value, a section on fisheries has been included.

The merlucciid material studied was acquired by the authors both fresh and frozen or obtained via museum collection exchanges.

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Hakes of the world (Family Merlucciidae). An annotated and illustrated catalogue of hake species known to date.


**ABSTRACT**

This is a worldwide catalogue of the family Merlucciidae. Two subfamilies, Macruroninae and Merlucciinae, are recognized comprising four genera, *Lyconodes, Lyconus, Macruronus* and *Merluccius,* and 18 species. The following subspecies are proposed: *Macruronus novaezelandiae magellanicus* Lönberg, 1907; *Merluccius albidos magnoculus* Ginsburg, 1954, *Merluccius australis polylepis* Ginsburg, 1954 and *Merluccius polli cadenati* Doutre, 1960 and *Merluccius merluccius smiridus* Rafinesque, 1810. The possibility of one other subspecies, *Merluccius merluccius lessepsianus,* represents the first record of *Merluccius* from the Red Sea. *Merluccius paradoxus* is first recorded from Madagascar.

In the introductory chapters, Merlucciidae systematics is debated, justifications for the proposed taxonomic organization are provided, and the characters used for the identifications are discussed.

Dichotomous keys are provided in the systematics chapter, enabling the identification of the hakes to the species level. Subfamilies and genera are also defined. The species are arranged in alphabetical order under each subfamily and genus to which they belong. The scientific name appears in bold at the head of each genus and species description, followed by the author, year of first description, and publication. Existing synonyms and FAO common names in English, French and Spanish are also provided. For each species there is an illustration followed by ten sections: description or diagnosis with differential characters; additional information; geographical distribution; habitat and biology; size; fisheries; fishery statistics; state of resources; local names, if any; and bibliographical references (author and year).

The review is completed by a series of colour plates showing details of different elements (heads, otoliths, hyomandibulars, urohyals) for a quick and efficient diagnosis of the genera and species of *Lyconus, Macruronus* and *Merluccius.*

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# TABLE OF CONTENTS

PREPARATION OF THIS DOCUMENT ........................................ iii
ABSTRACT ........................................................................ iv
ACKNOWLEDGEMENTS ................................................ iv

1. INTRODUCTION .................................................. 1
   1.1 Background .................................................. 4
       1.1.1 Merlucciidae Systematics ......................... 4
       1.1.2 Character Analysis at the Genus Level .......... 5
   1.2 Characters Subject to Variability ....................... 5
   1.3 Diagnostic Features of the Family ..................... 6

2. SYSTEMATIC CATALOGUE ............................................ 7
   2.1 Key to Subfamilies, Genera and Species (except the genus Merluccius) .......... 7
   2.2 Subfamily: Macruroninae Günther, 1873 .................. 7
       Lyconodes Gilchrist, 1922 ................................ 7
       Lyconodes argenteus Gilchrist, 1922 ............... 8
       Lyconus Günther, 1887 ................................ 9
       Lyconus brachycolas Holt and Byrne, 1906 ........ 9
       Lyconus pinnatus Günther, 1887 .................... 10
       Macruronus Günther, 1873 ............................ 11
       Macruronus capensis Davies, 1950 .................. 11
       Macruronus novaezelandiae (Hector, 1871) ........ 12
   2.3 Subfamily: Merlucciinae Svetovidov, 1948 ............ 14
   2.4 Key to Species and Subspecies of the Genus Merluccius .............. 16
       Merluccius Rafinesque, 1810 ....................... 17
       Merluccius albidus (Mitchill, 1818) ................ 18
       Merluccius angustimanus Garman, 1899 ........... 19
       Merluccius australis (Hutton, 1872) .............. 21
       Merluccius bilinearis (Mitchill, 1814) ............ 24
       Merluccius capensis Caspelau, 1861 ............... 26
       Merluccius gayi (Guichenot, 1848) ................. 28
       Merluccius hubbsi Marini, 1933 .................... 30
       Merluccius merluccius (Linnaeus, 1758) ......... 32
       Merluccius paradoxus Franca, 1960 ............... 35
       Merluccius patagonicus Lloris and Matallanas, 2003 .... 36
       Merluccius polli Cadenat, 1950 ................... 37
       Merluccius productus (Ayres, 1955) ............... 39
       Merluccius senegalensis Cadenat, 1950 ........... 40

3. LIST OF SPECIES BY MAJOR FISHING AREAS. .............. 42
4. BIBLIOGRAPHY .................................................. 44
5. INDEX OF SCIENTIFIC AND VERNACULAR NAMES ............ 53
6. COLOUR PLATES ................................................ 59
1. INTRODUCTION

In this review the family Merlucciidae has been divided into 2 subfamilies (Merluccininae and Macruroninae), which include four genera (Fig. 1) and 18 species. Amongst these species, commonly known as hake and grenadier, 13 are under the genus Merluccius and 2 in the genus Macruronus. These fishes are of great fishery interest and generally have a high commercial value.

The genus Merluccius is geographically widely distributed, although certain discontinuities appear in equatorial latitudes or their surroundings (Fig. 2). The genus is found in the Northern and Southern Hemispheres, on both sides of the Atlantic Ocean, throughout the eastern Pacific from a little north of the USA-Canadian border to Cape Horn, and off New Zealand; there are also periodic recordings of hakes in the western Pacific off Japan and in parts of the Indian Ocean south and southeast of Madagascar. Hakes are present along the European and African coast in the eastern Atlantic from the extreme north of the Scandinavian Peninsula and Iceland to the Cape of Good Hope; they are also found in the Mediterranean Sea, the southern part of the Black Sea, and are known from one isolated record in the Red Sea. On the western Atlantic coast of the Americas, hakes are found from Bell Island Canal (Newfoundland) in Canada to Cape Horn.

The genus Macruronus is less widely distributed and is only found in the Southern Hemisphere. They are found on each side of the Atlantic, with one record in the southern extremity of South Africa, but are more frequently encountered off the Argentinian coast. In the Pacific they are to be found off the coast of Chile, New Zealand, and to the south and east of Australia.

Hakes of the genus Merluccius constitute one of the most intensely exploited groups of demersal fish. They are primarily caught using bottom trawls, but also with gillnets and longlines. Some species, such as the Argentine hake, constitute targeted fisheries; others, such as the European and African hakes, are caught by multispecific fisheries, whilst in New Zealand they are accessory catches. Hake is a first-class fishery product; its quality and its subsequent commercial value differ significantly from one species to another. The excellent characteristics of the southern and European hakes give them a high market value if marketed whole and fresh. Other species of more inferior quality are gutted and filleted before being marketed and sold as diverse frozen products. Some species such as the North Pacific hake are difficult to market, owing to problems linked to their high level of parasites. Europe and Spain, in particular, constitute most of the world’s hake market, with imports up to 700 000 tonnes per year.

The total catch of Merluccius reported to FAO at the end of the twentieth century (Fig. 3a), amounted to approximately 1 200 000 tonnes; that of Macruronus amounted to more than 700 000 tonnes. For Merluccius, around two-thirds of world catch originates in the Atlantic Ocean (Fig. 3b), with the rest originating in the Pacific Ocean (Fig. 3c). Macruronus catches come almost entirely from the Pacific Ocean, except for around 137 000 tonnes caught in the Atlantic Ocean. Merluccius catches showed a strong increase at the beginning of the 1960s, reaching a maximum of just over 2 000 000 tonnes in 1973. Subsequent catches have fluctuated, showing a ten-year period when minimums registered in 1981, 1992, and 1999 amounted to almost 1 000 000 tonnes, and in 1986 and 1996 maximums reached almost 1 500 000 tonnes.
It is estimated that today’s hake fisheries offer no possibilities for expansion (Pitcher and Alheit, 1995). In most cases, overexploitation, to a greater or lesser extent, is to blame. Therefore, it is recommended that the present development strategy be modified in order to guarantee sustainability. It is, however, interesting to mention the resistance to fishing pressure shown by hake populations.

The family Merlucciidae as considered by Cohen et al. (1990) constitutes a problematic aggregation, and at present, there is no consensus concerning either its extension or its phylogenetic relations.

This lack of agreement affects the positioning and even the validity of some genera; as is the case for the inclusion or not of Lyconus in Macruronus and Lyconodes in Lyconus, or whether special treatment should be given to some species or subspecies of the genera Merluccius and Macruronus.

Numerous taxonomists have for a long time tried to include the species of Merluccius in a single dichotomous key. External morphological similarities of species have led to confusion, as experienced by Lozano Cabo (1965). In dealing with Atlantic hake, he states: “Existing differences amongst these hake are not easy to determine, even for specialists, leading one to seriously question whether they are in fact, different species”.

The situation becomes more complicated when economic interests come into play, as practically all the taxa of the genera Merluccius and Macruronus are objects of important fisheries, and processed and marketed. Statistical data generated with erroneous identifications complicate biological and fishery analyses.

For Merluccius, experience has shown that general identification keys available to date are inadequate when differentiating two or more congeneric entities present in the same geographic area, as is the case with specimens from the eastern and western Atlantic coasts and from the southern and eastern Pacific. It is even more so when identifying specimens of unknown origin.

To overcome this, various authors have put forward local or regional identification solutions in didactic or practical terms for the given entities.

As a result, there is a need to find concrete and stable differential characters. These should be, as far as possible, easily observable in order to permit rapid identification in a commercial fishery. When these characters are not obvious, the taxonomist has to resort to other more cryptic ones, which are often difficult to verify at a glance; internal anatomical or even genetic characters are then used. In any case, only visible characters can be used in keys.

The hierarchy which we here propose follows criteria established by Nelson (1994): Class Actinopterygii; Subclass Neopterygii; Order Gadiformes. However, the rank attributed to lower levels, such as family (Merluccidae), subfamilies (Macruroninae and Merlucciinae) as well as genera (Lyconodes, Lyconus, Macruronus and Merluccius), are based on the results obtained in the present study, regardless of other authors’ opinions.

![Genus Merluccius geographical distribution](image)
Fig. 3 Catch records of hakes (Merluccius spp.) and blue grenadier (Macruronus novazelandiae)
Finally, seeing as the fundamental objective of this publication is to draw up a key which uses visible characters, some information are not presented: raw data, details of all analyses carried out, and the description of the numerous material examined. We only retained information that, to our mind, best illustrates qualitative and meristic differences found between the species we have dealt with. In order to make up for any lack of information, a subsection entitled “Supplementary information” has been included at the end of each diagnosis. The keys proposed here were also verified and used to classify samples without heeding to their original cataloguing or origin and then verifying the validity of the identifications.

1.1 Background

In order to understand the process that led to this study, it is necessary to refer back to the sources that provide the different concepts on the composition of the family Merlucciidae. Although briefly touched upon in the introduction, it will be expounded on below.

1.1.1 Merlucciidae Systematics


Inada in Cohen et al. (1990) following Inada (1989) criterion, included *Merluccius* Rafinesque, 1810; *Macruronus* Günther, 1873; *Lyconus* Günther, 1887 and *Steindachneria* Goode and Bean, 1896 in the family Merlucciidae: the first three genera in the subfamily Merlucciinae and the fourth in Steindachneriinae. However, it must be pointed out that there is no existing consensus on the extent of the family Merlucciidae or whether it is a family as such, or simply a subfamily of the Gadidae. Even though all authors include in it the genus *Merluccius*, there are different opinions as to where *Macruronus*, *Lyconus*, *Lyconodes*, and *Steindachneria* belong.

Additional problems are whether to accept genus *Lyconodes*, as well as recent dissension on the validity of *Lyconus*.

Adams (1864) separated *Merluccius* from Gadidae and created for it the family Merlucciidae, which characters Gill (1884: 172-173) specified in the following way: “Gadoida with a moderate caudal region conform behind and with the caudal rays procurent forwards, the anus submedian, moderate suborbital bones, terminal mouth, subjugular ventral fins, dorsal double, a short anterior and long posterior one, a long anal corresponding to the second dorsal; ribs wide, approximated, and channelled before or with inflected sides, and paired excavated frontal bones with divergent crests continuous from the forked occipital crest.”

Günther (1887) included *Merluccius* in the Gadidae, *Macruronus* in Macrouridae, and created the family Lyconidae for *Lyconus*. Goode and Bean (1896) accepted the families Lyconidae and Merlucciidae, but included *Macruronus* and *Steindachneria* in Macrouridae.

Gilchrist (1922) described *Lyconodes*, a genus of controversial affinities but usually associated with *Lyconus*, and included it in the subfamily Lyconinae under the Coryphaenoidae. Barnard (1925) acted in the same manner.

Svetovidov (1948), in his revision of Gadiformes, considers Merlucciinae as a subfamily of Gadidae together with Lotinae and Gadinae.

Norman (1966) was the first to consider *Macruronus* and *Lyconus* as Merlucciidae, but in a subfamily of its own (Merlucciinae). Marshall (1966) and Cohen (1984) included them all in the family Merlucciidae made up of Merlucciinae (*Merluccius*), Macrurinae (*Macruronus*, *Lyconus* and *Lyconodes*) and Steindachneriinae (*Steindachneria*). According to Marshall (1966) the three subfamilies have the following in common: terminal mouth, front vomerine teeth biserial, 7 branchiostegals rays, the upper of which rests on the epihyal, pectoral fins with narrow base and 12 to 16 rays, ventral fins with 7 to 9 rays, and no barbel. The Merlucciinae have, among other characters, a separate caudal fin, second dorsal and anal fin of similar length and height, less than 30 vertebrae in the caudal region of the vertebral column, and prominent lower jaw; the Macrurinae and Steindachneriinae have dorsal and anal fins confluent caudally, dorsal-fin rays much longer than those of the anal, more than 30 caudal vertebrae, lower and upper jaw of equal length, and both with a few very long teeth; *Steindachneria* (Steindachneriinae) is singular in having the anus located between the pelvic fins and clearly separated from the urogenital orifice, which is located just before the anal fin, and also for possessing a complex bioluminescent system.

Marshall and Cohen (1973), Fahay and Markle (1984), and Okamura (1989) separate *Steindachneria* into a family (Steindachneriidae) and put the rest of the aforementioned genera in Merlucciidae. Nolf and Steurbaut (1989) came to a similar conclusion by analysing otoliths, but included them, respectively, in Steindachneriinae and Merlucciinae, within the Gadidae.

Using osteological and ontogenetic characters, Fahay (1989) separated *Steindachneria* from Merlucciidae and related them to the Macruroidae. Markle (1989) spoke of three families: Steindachneriidae, as monotypic and under Macruroidei, whereas Merlucciidae, also monotypic, and Macruridae (*Macruronus* and *Lyconus*) are grouped under Gadoidei.

Howes (1991) states “Presumed synapomorphies relating *Macruronus* and *Merluccius* are shown to be homoplastic. *Macruronus*, *Lyconus* and possibly *Lyconodes* form a monophyletic group recognized as family Macruridae, *Merluccius* is the sole member of Merlucciidae.” Steindachneriidae would also be monotypic.

As can be seen, at present there is no consensus on the extent of the family Merlucciidae. An in-depth revision of all genera that could be part of it is necessary.
1.1.2 Character Analysis at the Genus Level

In order to classify genera, the criteria of Marshall and Cohen (1973), Fahey and Markle (1984), and Okamura (1989) have been adopted so that Merluccidae is divided into 2 subfamilies: Merluccini and Macruroni. whose affinity and differential characteristics can be seen in the adjoining identification key for subfamilies and genera.

In this way, Merluccini includes only the genus *Merluccius*, while *Lyconodes*, *Lyconus*, and *Macruronus* constitute the Macruroni. Among these, *Lyconodes* and *Lyconus* are closely linked, which leads to the possibility of them belonging to the same genus. However, owing to the lack of information, especially concerning *Lyconodes*, we are inclined to respect the present dichotomy.

This is not the end of the difficulties to be sorted out. Various entities in *Macruronus* and *Merluccius* at the species and subspecies levels remain to be identified. Meristic characters that have been used up until now are highly variable and largely overlap between different species.

1.2 Characters Subject to Variability

The most common method used by taxonomists to group organisms into different taxa is to study anatomical, meristic, and morphometric characters in a comparative manner.

As mentioned in the background section, taxonomic knowledge of *Merluccius* has posed, and still poses, serious difficulties in separating its different entities into possible species or subspecies. This is due, among other things, to the fact that the characters used for comparison largely overlap. The same applies to *Macruronus* and, to a lesser extent, to the rest of the genera included in the Merluccini.

As for *Merluccius* and *Macruronus*, it has to be said that in practice the vast majority of authors have used meristic characters, such as the number of fin rays, vertebrae, lateral-line scales, and number of gillrakers of the first arch. According to Ginsburg (1954), this is due to “...the greatest divergence in proportional measurements in *Merluccius* seems to be shown by the smaller size groups. With growth, the extent of divergence appears to become lessened and perhaps disappears in some instances.” We therefore agree with Franca (1962), who states that metric characteristics are of no or of secondary value for a correct determination. Some meristic characters, however, said to be reliable for species identification (rays, vertebrae, scales and gillrakers) are subject to high variability in relation to trophic or clinal conditions. This renders them unsuitable, as they require the use of large numbers of observations to obtain different modal values of samples to compare; therefore, large overlap and ambiguities lead to permanent confusion.

Geographical latitude is often linked with variation in the number of vertebrae, which in part is true. In general, cold, temperate, or warm superficial waters are, respectively, related to high, medium, and low latitudes. However, deep waters, generally of lower and more uniform temperature, may rise to the surface in tropical or subtropical regions and influence the embryonic development of species spawning in the area, independent of their geographical latitude.

Jordan’s Law (Jordan 1921) is generally accepted. It states that there is an inverse relation between the number of vertebrae and temperature, that is, the lower the water temperature, the higher the number of vertebrae, and vice versa. Interest was aroused a few years earlier with Jordan (1891, in Vega, 1987) and Heincke (1898) in Margalef, (1974), whereby the average number of vertebrae of individuals in a population was put forward as criteria to distinguish races in herrings and Labridae.

There are other factors also linked to temperature that influence the variability in the number of vertebrae, for example: egg size, which is larger in colder waters (Marshall, 1953; Hempel and Blaxter, 1961 in Margalef 1974), photoperiod (Fowler, 1970), and salinity (the lower the salinity, the lower the number of vertebrae).

On the other hand, Jordan’s Law, relative to the vertebrae of fishes is a particular case of a much wider phenomena of variation that affects not only the number of vertebrae, but also the fin rays, gillrakers, photophores and the number of scales on the lateral line (Hart, 1937; Tester, 1938; Tanning, 1951; Andreu et al., 1952; Andreu, 1969; Margalef, 1974).

It should be pointed out that, the number of vertebrae is more important from the point of view of the pleomorism rule, in which Lindsey (1975) demonstrated in 118 fish families a positive correlation between the number of vertebrae and their maximum size.

However, various authors still use the number of rays, vertebrae, gillrakers, and lateral-line scales as differentiating species characters. It is important to note that although such parameters are occasionally useful in determination keys, they are merely of complementary value and should by no means be used as distinguishing criteria to characterize an entity at the species level.

In this respect, Angelescu et al. (1958), in their exhaustive work on Argentine hake (*Merluccius hubbsi*), conclude that meristic characteristics cannot be used as specific separation indices, but only as a subspecific value.

It is worth mentioning that when dealing with numerical values, such as number of scales, rays, vertebrae, or gillrakers, the mode should be preferred to the mean, as it relates to the frequency and therefore the possible normality of the character.

Leible (1974) revealed comparative problems when he made reference to the method of vertebral counts used by different authors. Some do not indicate whether the urostyle is included or not. Cadenat (1952), Maurin (1954), Doutre (1960) and Franca (1962) include it, while Gall (1952) in Arana (1970) does not.

The presence or absence of vomerine and palatine teeth in Merluccidae has also contributed to the confusion. Thus, while Goode and Bean (1896), with the majority of authors, indicate the presence of teeth on the vomer and their absence on the palatine, Poli (1953: 209) wrongly indicates the presence of palatine teeth.
Confusion also occurs with the relative position of the ventral fins, one of the differentiating characters of the genera *Merluccius* and *Macruronus*. For *Merluccius*, ventral fins are inserted before the pectoral fins in a subjugular position, as indicated by Goode and Bean (1896), Belloc (1929), and Fowler (1936); others such as Lozano Cabo (1952), Poll (1953), and Angelescu (1958) consider them as being jugular. Inada (1981b) and Inada in Cohen *et al.* (1990) say they are thoracic.

Authors’ opinions differ with regard to certain internal characters of the Merlucciidae, as for example, the presence or absence of pyloric caeca in *Merluccius*. Thus, Belloc (1929), Fowler (1936), and Lozano Rey (1960) indicate that they have one, whereas various modern authors (Inada, 1981b and Inada in Cohen *et al.*, 1990) do not mention them. In our case, the presence of a pyloric caecum in samples of different Euro-African and American species was observed.

Moreover, the problem is heightened when different authors assign to a single binomen all specimens coming from a given location. Errors are also made with direct transcription from one author to another, without prior verification.

With respect to this, for the present revision, data were taken directly from samples coming from different type localities, except for *Macruronus capensis*, *Lyconus pinnatus* and *Lyconodes argenteus*, for which we only had access to the existing literature.

Finally, key validity has been verified by identifying individuals without heeding their classification or provenance.

### 1.3 Diagnostic Features of the Family

Body fusiform, elongated, and rather compressed, especially in the caudal region. Caudal peduncle well differentiated (Fig. 4 and Plate I) or non-existing with union of the dorsal, caudal and anal fins (Fig. 5 and Plate I). Anal and urogenital openings adjoining. Head generally large, with a V-shaped ridge on the dorsum opening towards the front (Fig. 6). Scales cycloid and deciduous, without asperites. Lateral line present. Branchiostegal rays 7. Branchial openings wide. With or without pseudobranchs. Large, terminal, oblique mouth with lower jaw generally somewhat protruding, and without barbels. Strong sharply pointed teeth on premaxillary, lower jaw and vomer, but not on the palatines. One or 2 dorsal fins; when two are present, the first one is short based and the second long. A single anal fin similar in length to, or shorter than, the second dorsal fin. Pectoral insertion variable in position, with the first ray at the level of the centre of the eye or clearly below. Ventral fins with 7 to 10 rays, inserted slightly before pectoral fins (subjugular), at the same vertical (thoracic), or even slightly behind them. Caudal fin sometimes separated from dorsal and anal fins and sometimes attached. Except for the first dorsal ray, all rays are articulated and none are filiform. Swimbladder physoclistous. One or multiple pyloric caeca.

Demersal and benthopelagic fishes characteristic of cold or temperate waters, feeding on a large variety of prey. The family is made up of 2 subfamilies: *Macruroninae* and *Merlucciinae*, comprising 4 genera and 18 species.

The abbreviations used in the description of each species are the following: 1D., first dorsal fin; 2D., second dorsal fin; A., anal fin; P., pectoral fin; V., ventral or pelvic fin; Gr., total number of gillrakers on the first gill arch; L.L., number of scales on the lateral line; TV., total number of vertebrae; CV., number of cervical vertebrae; CR., number of cervical ribs. For meristic values and biometric%ages, all observed ranges obtained by previous authors as well as those from the current study are provided and recorded as minimum and maximum values, and when available, the mode in brackets.