

The houting *Coregonus oxyrinchus* (L.) (Salmoniformes: Coregonidae), a globally extinct species from the North Sea basin

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Coregonus oxyrinchus is redescribed and a neotype is designated (BMNH 1862.11.20.1.). It was restricted to south England and the lower parts of the Rivers Rhine, Meuse and Schelde. It is now globally extinct; the last individual was caught in 1940. *Coregonus oxyrinchus* is distinguished from other coregonids by having 38–46 gill rakers and a long, pointed snout.

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Key words: extinction; houting; North Sea; taxonomy.

INTRODUCTION

The loss of biodiversity represents a deficit to present and future generations. Modern European concepts of nature conservation (EWG, 1997) highlight the responsibility of governments to study and conserve endemic and endangered species of plants and animals. The houting *Coregonus oxyrinchus* (L.) is listed as a species of priority interest to nature conservation in Europe (EWG, 1997). The distribution and conservation status of this species, however, seem to be only vaguely known. *Coregonus oxyrinchus* has usually been considered to be restricted to the North Sea basin (Landois, 1892; Thienemann, 1922; Ladiges & Vogt, 1979), marginally including the North Sea, and perhaps also the western part of the Baltic basin (Siebold, 1863; Bade, 1902; Vogt & Hofer, 1909; Schindler, 1953; Svårdson, 1979). Concerns have been raised, however, that the range of *C. oxyrinchus* may be more restricted. Redeke (1934) and Thienemann (1937) pointed out that houting from the River Rhine delta could be differentiated from those of the River Elbe and the rivers entering the Baltic Sea by the numbers of gill rakers and the shape of the snout. Both authors stated that two species might have been confused under the single name *C. oxyrinchus* (houting).

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In the lower Rhine, the houting population started to decline during the late 19th century and collapsed in the first three decades of the 20th century due to pollution and overfishing (Lelek & Buhse, 1992). The last specimens were caught in the lower Rhine in 1940 (Bauch, 1958; Lelek & Buhse, 1992). In recent years, re-introduction of fishes has become very popular among angling societies. Attempts at re-introduction of houting to the Rhine began in 1992 with fish originating from the River Vida, Denmark (Freyhof, 2002). The main aim of the present study is to re-examine historical and recent anadromous coregonids from the rivers draining to the southern part of the North Sea and south-west part of the Baltic Sea in order to reconstruct the original distribution of *C. oxyrinchus*. The second aim is to review the opinions of Redeke (1934) and Thienemann (1937) that fishes usually identified as *C. oxyrinchus* actually represent two species. If this is true, then the fish 're-introduced' in the Rhine from Denmark (North Sea basin) would not be the native *C. oxyrinchus*, but probably the non-native *Coregonus maraena* (Bloch) and the threatened *C. oxyrinchus* would have to be moved to the list of globally extinct species.

MATERIALS AND METHODS

Fourteen complete specimens and two heads of the historical material of *C. oxyrinchus* from the lower Rhine, Meuse and Schelde drainages (North Sea basin) were examined. This apparently represented most of the existing material of *C. oxyrinchus*; additional material known is a dry skin and a complete specimen in the Natural History Museum, London, and a complete specimen in Muséum National d'Histoire Naturelle, Paris. Additional material of other anadromous and riverine *Coregonus* species from the Rhine and other rivers of the North Sea and western Baltic basins (Fig. 1) were also examined ($n = 138$; see Appendix for specimens examined). Measurements were taken directly from specimens using dial calipers. Measurements and counts follow those of Fang (1997) and Schulz & Freyhof (2003). Differences in gill raker counts were tested using an ANOVA table including a Dunnett T-3 *post hoc* test, and sequential Bonferroni adjustment (Rice, 1989). Following the Bonferroni adjustment, significance was obtained with a $P < 0.003$. Morphometric characters and institutions are denoted by the following abbreviations: L_S , standard length; BMNH, Natural History Museum, London; FSJF, Fischsammlung Jörg Freyhof, Berlin; GNM, Göteborg Natural History Museum, Göteborg; MNHN, Muséum National d'Histoire Naturelle, Paris; NMBE, Naturhistorisches Museum Bern; NMW, Naturhistorisches Museum Wien; RIVO, Nederlands Instituut voor Visserijonderzoek; ZMA, Zoologisch Museum Amsterdam; ZMB, Museum für Naturkunde der Humboldt-Universität, Berlin; ZMUC, Zoological Museum, University of Copenhagen; ZSM, Zoologische Staatssammlung München.

RESULTS

The anadromous and riverine coregonids examined can be grouped according to the presence or absence of a prominent snout and inferior mouth. By this character *C. oxyrinchus* is well distinguished from the specimens of *C. widegreni* Malmgren and *C. sp.* 'Rhine', which do not have a prominent snout and subinferior mouth. *Coregonus oxyrinchus* collected between 1844 and 1906 from lower Rhine, Maas and Schelde have 38–46 gill rakers on the first branchial arch. In contrast, specimens identified as *C. oxyrinchus* collected from North Sea tributaries east of the River Rhine and Baltic basin, and in the lower Rhine after 1998, have 23–35 gill rakers on the first branchial arch

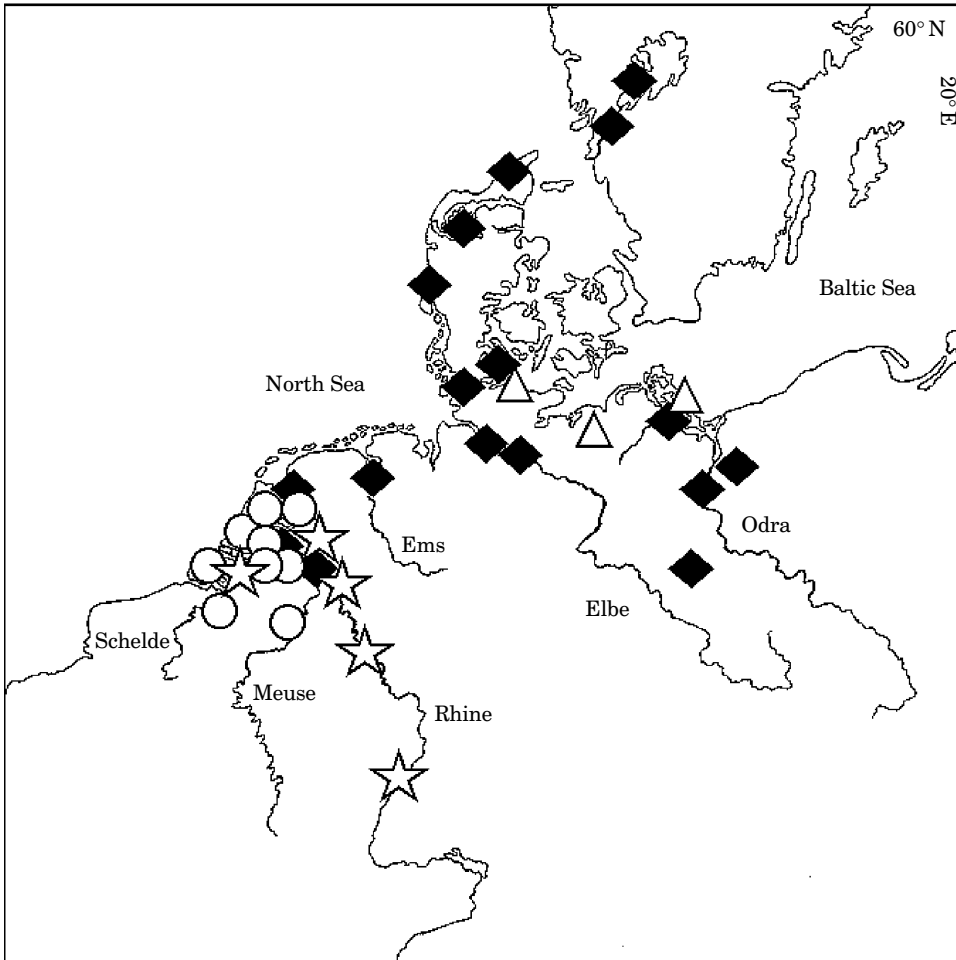


FIG. 1. Locations of examined *Coregonus* spp. (○, *C. oxyrinchus*; ◆, *E. maraena*; ☆, *C. sp.* 'Rhine'; △, *C. widegreni*) in North and Baltic Sea basins.

(Fig. 2). To help identification of the different species, a redescription of *C. oxyrinchus* is given below. The type locality of *C. oxyrinchus* is apparently the North Sea in the vicinity of Leiden (see below) and, according to the neotype designation below, specimens of *Coregonus* from this region with high number of gill rakers belong to *C. oxyrinchus*. *Coregonus* with lower numbers of gill rakers are identified as *C. maraena*. In *C. maraena* from North Sea and Baltic basins, the ranges in gill raker counts are large with overlaps (Fig. 2). Statistical analysis (ANOVA including Dunnett T-3 *post hoc* test) followed by Bonferroni adjustment reveals significant differences ($P < 0.001$) in gill raker counts between those populations (Table I). Despite this, the range in gill raker number shows some overlap between the two populations and so the specimens cannot always be distinguished according to these differences. It is beyond the aim of this study to solve the complex problems related to the diversity within

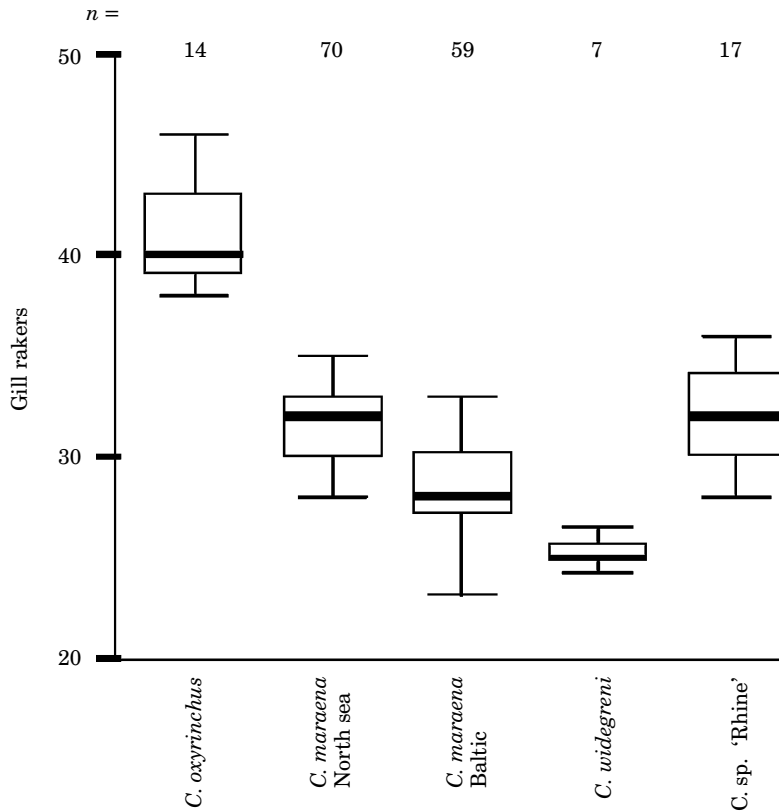


Fig. 2. Box-plots of gill raker counts of *Coregonus* spp. from the North Sea and Baltic basins, showing median, 25% and 75% percentiles and smallest and largest values.

C. maraena. Thus far, two or more diagnosable groups could not be found within this material.

COREGONUS OXYRINCHUS (L., 1758)

Diagnosis

Coregonus oxyrinchus is distinguished from all other species of *Coregonus* in Europe by having a long, pointed snout, an inferior mouth and 38–46 gill rakers.

Redescription: *Coregonus oxyrinchus* is now redescribed [see Fig. 3(a), (b) for external appearance and Table II for morphometric data of the neotype (BMNH 1862.11.20.1) and 13 additional specimens examined].

Large, elongate and strongly laterally compressed coregonid species. Mouth inferior, with maxilla reaching beyond anterior eye margin, often to centre of eye. Upper jaw projecting beyond lower jaw, mandible reaching posteriorly beyond centre of eye. Eye large, its diameter 0.6–1.0 (mean 0.7) times in inter-orbital width. Caudal peduncle 1.3–1.9 (mean 1.6) times longer than deep. Dorsal fin margin concave. Pelvic fin origin below branched dorsal fin ray 2–3.

TABLE I. *P* values for ANOVA and *post hoc* tests for number of gill rakers in different samples and species of *Coregonus* examined

	<i>Coregonus oxyrinchus</i>	<i>Coregonus maraena</i> North Sea	<i>Coregonus maraena</i> Baltic	<i>Coregonus maraena</i> Lake Miedwie	<i>Coregonus maraena</i> Lake Vänern basin	<i>Coregonus widegreni</i>
<i>Coregonus maraena</i>	0.000*					
North Sea						
<i>C. maraena</i>	0.000*	0.000*				
Baltic						
<i>C. maraena</i>	0.000*	0.993	0.961			
Lake Miedwie						
<i>C. maraena</i>	0.000*	0.047	0.972	0.749		
Lake Vänern basin						
<i>C. widegreni</i>	0.000*	0.000*	0.361	0.222	1.000	
<i>C. sp. "Rhine"</i>	0.000*	1.000	0.038	1.000	0.174	0.001*

*, significant difference after Bonferroni adjustment.

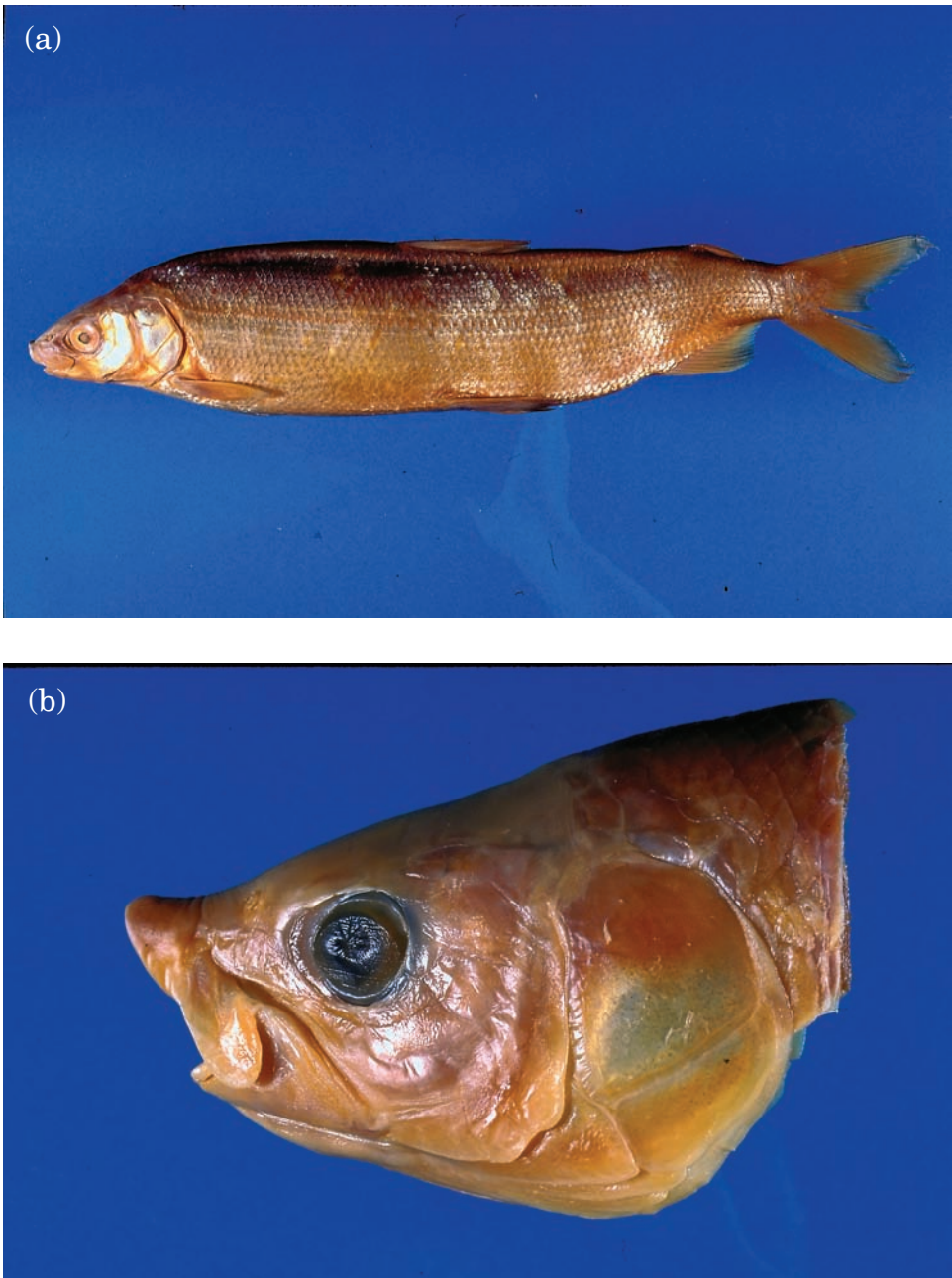


FIG. 3. (a) *Coregonus oxyrinchus*, BMNH 1862.11.20.1, neotype, 306 mm L_S ; Belgium: Antwerp, River Schelde. Lateral view. (b) *Coregonus oxyrinchus*, ZSM 25478, 80mm L_H , the Netherlands, River Rhine. Lateral view of the head.

Gill rakers 14–16 (mode 15) on upper part of first gill arch, 25–30 (mode 26) on lower part, 38–46 (mode 40) total. Juvenile specimen (148.5 mm L_S) from south England with 36 gill rakers. Length of last gill raker on upper part of first gill

TABLE II. Morphometric data of neotype of *Coregonus oxyrinchus* (BMNH 1862.11.20.1.) plus 13 additional specimens (BMNH 1844.11.11.15, NMBE 1020331, MNHN B-2497,0000-1502, ZMA 108.138, 123.602, 123.602, 123.602; MNHN 0000-2786, ZSM 4898, ZMA 123.601, 123.601). Additional morphometric data of head measurements of ZSM 25478 ($n = 2$) included

	Neotype	Mean	Minimum	Maximum	S.D.
L_S (mm)	306.0	229.4	129.8	323.0	-
Per cent of L_S					
Lateral head length	62.6	21.1	19.7	22.9	0.8
Predorsal length	148.2	48.5	45.9	53.1	1.7
Prepelvic length	161.0	52.5	49.6	56.0	1.7
Preanus length	246.5	76.9	72.5	79.1	1.9
Preanal length	239.0	78.9	74.4	81.6	1.9
Preadipose length	160.0	84.3	82.1	87.3	2
Prepectoral length	57.7	20.5	19.1	23.3	1.1
Body depth at dorsal-fin origin	67.6	23.0	20.9	26.6	1.5
Depth of caudal peduncle	21.7	7.6	7.0	8.4	0.5
Length of caudal peduncle	28.5	12.1	9.4	14.0	1.3
Length of dorsal-fin base	40.5	12.6	11.0	14.7	1.2
Length of dorsal fin	45.5	16.8	14.9	18.3	1.1
Length of upper caudal-fin lobe	50.5	16.6	15.0	17.8	1.2
Length of middle caudal-fin ray	27.5	8.8	7.1	10.3	0.9
Length of lower caudal-fin lobe	52.2	13.8	0.0	17.8	6.9
Length of anal fin base	37.7	11.5	9.4	14.4	1.3
Length of anal fin	31.9	11.3	9.9	15.7	1.6
Length of pelvic fin	44.7	14.5	13.1	15.4	0.7
Length of pectoral fin	36.5	12.7	0.0	14.8	3.7
Per cent of L_H					
Eye diameter	13.3	19.7	16.7	22.4	1.7
Eye height	12.4	18.6	16.5	23.0	1.6
Interorbital width	18.9	28.9	24.7	33.1	2.1
Inter-nares distance	7.4	12.2	8.9	14.7	1.7
Eye-nare distance	7.9	11.9	10.1	13.6	0.9
Snout length	21.4	33.1	28.4	40.8	4.1

L_S , standard length; L_H , head length.

arch 76-111 (mean 92) % of length of opposite gill filament. Largest recorded specimen 470 mm L_S .

Dorsal fin with 4-5 (mode 4) unbranched and 9-12 $\frac{1}{2}$ (mode 11 $\frac{1}{2}$) branched rays. Caudal fin forked, with 9 + 8 branched rays, 8 + 8 and 7 + 8 branched rays in one specimen. Anal fin with 4 unbranched and 10-12 $\frac{1}{2}$ (mode 11 $\frac{1}{2}$) branched rays. Pectoral fin with 1 unbranched and 12-15 (mode 13) branched rays. Pelvic fin with 2 unbranched and 9-11 (mode 10) branched rays. Axillary pelvic lobe present. Lateral line complete, reaching caudal-fin base, perforating 74-83 (mean 79) scales on body and 4-6 (mode 4) on caudal fin base. Scales between lateral line and dorsal-fin origin 9-10 (mode 9), and pelvic fin origin 7-9 (mode 8), and anal fin origin 7-8 (mode 8). Scales around caudal peduncle 21-25 (mode 22).

Ecological data presented by Redeke (1934) suggest that *C. oxyrinchus* is a planktivorous species not migrating to pure marine waters. *Tripteronotus hautin* La Cepède is the only synonym of this species (Kottelat, 1997).

KEY TO SPECIES OF RIVERINE AND ANADROMOUS
COREGONUS IN NORTH SEA AND WESTERN BALTIC BASIN

1. – Snout long, conical, noticeably extended anteriorly beyond the lower jaw, at least in mature males [Fig. 4(a)]. 2
 - Snout short, not conical, only slightly extended anteriorly beyond the lower jaw [Fig. 4(b)]. 3

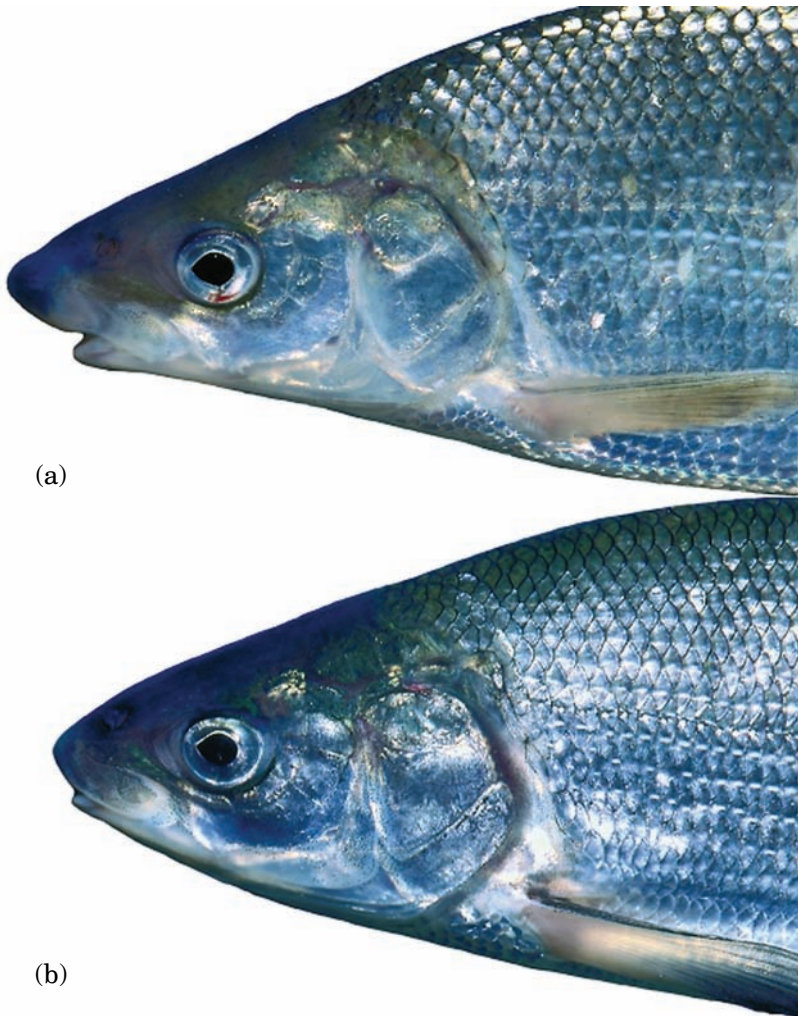


FIG. 4. (a) *Coregonus maraena*, FSJF 521, 330 mm L_S , Germany, River Odra and (b) *Coregonus widegreni* FSJF 525, 390 mm L_S ; Germany: Lake Drewitzer. Lateral views of the head.

2. – 38–46 gill rakers on the first branchial arch. *C. oxyrinchus*
– 23–35 gill rakers on the first branchial arch. *C. maraena*
3. – Dorsal profile increasing to middle of distance from nape to dorsal-fin origin, straight from that point to dorsal-fin origin; 20–26 gill rakers on the first branchial arch; estuarine, migrating only few kilometres beyond the brackish water region. *C. widegreni*
– Dorsal profile continuously increasing from nape to dorsal-fin origin; 30–36 gill rakers on the first branchial arch; riverine, not found in estuaries. *C. sp.* ‘Rhine’

DISCUSSION

NOMENCLATURE

Salmo oxyrinchus was first described by Linnaeus (1758), but no type material was explicitly mentioned. The description was based on two earlier literature accounts, namely Artedi’s (1738) description of *Coregonus maxilla superiore longiore conica* and Gronovius’ (1754) description of *Salmo unicolor albescens*. Artedi’s (1738) account is based on his own observations, and on literature accounts by Rondelet (1555), Gesner (edition not stated, apparently 1563), Aldrovandri (1613), Jonston (1649), Charleton (1668), Willughby (1686) and Ray (1710). Gronovius’ (1754) account is based on his own observations and literature accounts by Artedi (1738), Klein (1749), Linnaeus (1746; 1748), Ray (1710) and Willughby (1686). Rondelet (1555: 141) was the first who mentioned a fish as *Oxyrinchus*. Subsequent authors such as Gesner (1563), Charleton (1668), Willughby (1686) and Ray (1710) simply copied Rondelet’s account and figure.

Gronovius (1754) included two species from Ray (1710) in his account: namely *Oxyrinchus* which Ray (1710) copied from Gesner (1563), who in turn copied it from Rondelet (1555), and *Albula nobilis* which Ray (1710) copied from Schoenfelde (1624). Based on material from the estuarine River Elbe, the rivers of Holstein (Germany) and from Denmark, Schoenfelde (1624) described and illustrated a fish as *A. nobilis* known under the name Snepel in Germany and Snebbel in Denmark. In this area, Schnäpel is the common name of this fish today. Schoenfelde’s *A. nobilis* is clearly identical with *Coregonus maraena* as described by Bloch (1779). Indeed, Schoenfelde (1624) and Artedi (1738) treated *Oxyrinchus* and *A. nobilis* as two species. Artedi (1738), however, incorrectly included Schoenfelde’s *A. nobilis* in his account of *Coregonus maxilla superiore longiore plana*, which was later included in *Coregonus lavaretus* by Linnaeus (1758).

The fact that Gronovius (1754) included Ray’s (1710) reference to *Oxyrinchus* (= *C. oxyrinchus* from Rondelet) and *A. nobilis* (= *C. maraena* from Schoenfelde) in his description of *Salmo unicolor albescens* means that these two different species were also included in *C. oxyrinchus* as originally described by Linnaeus (1758). Linnaeus’ short description does not indicate whether his notion of *C. oxyrinchus* was closer to Rondelet’s *Oxyrinchus* or Schoenfelde’s *A. nobilis*. It is necessary therefore, to designate an appropriate

lectotype or neotype to restrict Linnaeus' *C. oxyrinchus* to one of these two species.

NEOTYPE DESIGNATION

Because Linnaeus did not explicitly mention a type specimen in his original description of *C. oxyrinchus*, all specimens included by Linnaeus (whether directly or by bibliographic reference) become syntypes (ICZN, 1999: art. 72.2 and art. 73.4). Whether they still exist or not is irrelevant to their status as syntypes. Therefore, the specimen figured as *Oxyrinchus* by Rondelet (1555), and the specimen figured as *A. nobilis* by Schoenfelde (1624), are both syntypes of *C. oxyrinchus*.

Problems might arise because of the uncertainties surrounding the identification and possible syntype status of the specimen BMNH 1853.11.12160. Wheeler (1958:208) identified BMNH 1853.11.12160 in the Gronovius' fish collection as one of the individuals examined for Gronovius' *Museum ichthyologicum* (1754), therefore this is the only known, existing specimen which might be a syntype. Unfortunately, Gronovius always removed the gills, while preparing the fish for conservation (Wheeler, 1958). Therefore, one of the most important diagnostic characters is lost (J. Maclaine, pers. com.), and it is impossible to identify this specimen correctly, and so confirm whether Gronovius might have used it for his description of *Salmo unicolor albescens*.

According to Gronovius (1754) his *Salmo unicolor albescens* originated from the northern sea (Mare septentrionale). His specimen may have been obtained from markets in Leiden where Gronovius spent most of his life, but this cannot be proven. Because the origin and identity of Gronovius' specimen is uncertain, it does not qualify as a suitable lectotype. Instead, it is designated here as lectotype the specimen on which Rondelet's (1555: 141) figure of 'Hautin' is based. Rondelet (1555) explicitly stated that he knew this species from Antwerp (Anvers), where it is called hautin. This is exactly the same name and spelling Artedi (1738) mentioned for his *Coregonus maxilla superiore longiore conica*, and this name is very similarly written and pronounced as the 'houting' (De Nie, 1997) in contemporary Dutch language. Artedi (1738) noted *Coregonus maxilla superiore longiore conica* as from 'Flandria and Batavia', both being within the River Rhine, Meuse and Schelde delta, including the region around Antwerp [Flandria represents today's Belgian province of Vlanderen, and Batavia represents the Dutch provinces of Zeeland and Zuid-Holland (Menge, 1988; Kinder & Hilgemann, 1992)].

Rondelet is not known to have preserved any material and no museum material has ever been claimed as collected or examined by Rondelet. The lectotype designated above is, therefore, no longer extant and a neotype of known origin and exhibiting the diagnostic characters of *C. oxyrinchus* is now designated.

ICZN (1999) art. 73.3.6 requires that the neotype comes from a location as close as practicable from the original type locality, meaning from Antwerp. Specimen BMNH 1862.11.20.1., 306 mm L_S (Fig. 3a), collected in the River Schelde in the Province Antwerp (Belgium), is now designated as neotype of *Coregonus oxyrinchus* Linnaeus, 1758. Linnaeus' description is mostly

uninformative, however, it is clearly stated in Artedi's description (on which Linnaeus' is based in part) that the species has a long, conical snout (*Coregonus maxilla superiore longiore conica*) and this feature is evident in the neotype, allowing its identification as *C. oxyrinchus*. By this neotype designation, the name *C. oxyrinchus* (Linnaeus, 1758) is definitively restricted to the species known from England and the lower parts of the Rivers Rhine, Meuse and Schelde, and the use of the name is stabilized.

SYSTEMATICS

The results of this study confirm Redeke's (1934) and Thienemann's (1937) conclusion that two species of long snouted coregonids are known from the North Sea basin: *C. oxyrinchus* in England, the Rhine, Meuse and Schelde, and *C. maraena* migrating along the rivers east of the Rhine (but also in the Baltic basin).

Coregonus oxyrinchus is a very distinctive species, different from the anadromous coregonids tentatively identified as *C. maraena* and *C. widegreni* by Kottelat (1997) (see above), and from all prealpine species (Vogt & Hofer, 1909). In fact, there is no similar long-snouted *Coregonus* in Europe and the east coast of North America (Boschung *et al.*, 1988).

Thienemann (1937) tried to accommodate the distinctive combination of characters (long snout and high number of gill rakers) by considering *C. oxyrinchus* as a subspecies of *C. generosus* Peters, 1875 (*C. generosus oxyrinchus* is a lapsus because *C. oxyrinchus* has priority over *C. generosus*). Svårdson (1979) tried to explain the combination of characters as a result of hybridization between the long-snouted Baltic *C. maraena* (with low gill raker number) and the short-snouted 'Plantonsik' *C. nilssoni* (with high gill raker number). There is neither description nor historic material, however, proving that *C. nilssoni* ever occurred in the Rhine; further it would be unusual for a hybrid to simply combine characters of two species instead of exhibiting intermediate character states.

Another, as yet unidentified riverine *Coregonus* occurs in the River Rhine that is not conspecific with *C. nilssoni*, *C. oxyrinchus* or *C. maraena*. It is here called *Coregonus* sp. 'Rhine'. This species has a short snout and usually 30–36 gill rakers. Its presence in the Rhine is usually considered to represent escapees from stocks introduced to reservoirs or individuals washed out from prealpine lakes for unknown reasons. In the area of Strasbourg (France), there have been records of this species as early as 1666 (Lauterborn, 1903), including records of its spawning. At Phillipsburg, 90 km north of Strasbourg, juveniles and fully ripe specimens were observed in 1996, indicating that this *Coregonus* species still reproduce in the Rhine (U. Weibel, pers. comm.). Preserved material examined has not yet been properly identified. This is due to the unresolved systematics of most Swiss coregonids and the possibility that it belongs to one of these Swiss species. Molecular markers might help to resolve the identity of this species. Unfortunately, only formalin preserved specimens of *Coregonus* sp. 'Rhine' have been available.

The only confirmed records of *C. oxyrinchus* are from England and the Rivers Rhine, Meuse and Schelde, and this species was apparently endemic to that area.

Specimens of *Coregonus* from all drainages east of the Rhine that were examined in this study are *C. maraena*. Statistical differences in gill raker counts among populations of *C. maraena* from the Baltic and North Sea basin east of the Rhine are not large but are significant. Hansen *et al.* (1999) studied mitochondrial DNA and microsatellite markers of *C. maraena* from the Baltic and North Sea basins and found small differences; they suspected that these populations might have been isolated by postglacial events. It cannot be excluded that Baltic and North Sea populations of *C. maraena* are separate species, resulting from postglacial isolation, but this requires further investigation before it can be confirmed.

ZOOGEOGRAPHY

The distribution area of *C. oxyrinchus* is usually reported to include south-east England. This is based on records of single specimens collected from Lincolnshire in 1877, Chichester in 1880, and the mouth of the River Medway in 1881 (Day, 1880–1884). It was possible to find one uncatalogued specimen in the BMNH (148.5 mm L_S) labelled as coming from the ‘South Coast of England’ and acquisition details are ‘F. Day Esq.’. This specimen has a long and pointed snout and 36 gill rakers, confirming Day’s identification and demonstrating that *C. oxyrinchus* was present at the English coast. Regan (1911) reported this species in England only from markets, where it was imported from the Netherlands. There have been no subsequent records, or records of a reproducing population, from England (Maitland, 1970). Redeke (1934) noted that he had never found *C. oxyrinchus* in pure marine water in the Netherlands. Therefore, this species probably does not normally leave estuarine waters and it is unlikely that it has colonized British waters by marine dispersal from continental European rivers. It seems likely that records by Day (1880–1884) represent relict populations that had dispersed to in southern England in early glacial periods, when there was less of a marine barrier, and then became extinct in the late 19th century.

Coregonus oxyrinchus seems to be the only fish species endemic to the lower Rhine, Meuse and Schelde basin and south-east England (Ladiges & Vogt, 1979; Lelek & Buhse, 1992). Molecular studies, however, have revealed that two lineages of *Cottus gobio* (L.) probably survived the last glaciation in the lower Rhine (Englbrecht *et al.*, 2000) and Schelde (Volckaert *et al.*, 2002), which might have been a glacial refuge area for some cold adapted freshwater fish species. During the last glaciation, the lower Rhine basin drained through the English Channel into the Atlantic Ocean whereas the glacial River Elbe drained to the north-east and was isolated from the Rhine (Hantke, 1993). Danish North Sea tributaries, as well as the Rivers Ems and Weser drained to the glacial River Elbe (Hantke, 1993). Hansen *et al.* (1999) already suspected *C. maraena* to have had at least one refuge in this glacial River Elbe, colonizing the Baltic basin after the postglacial opening of the connection between the Baltic and the North Sea. It cannot be excluded, however, that two different species are currently being confused under the name *C. maraena*: the true, lacustrine *C. maraena* from the type locality (Lake Miedwie, Poland) and another, anadromous species in Baltic drainages.

CONSERVATION STATUS

From this analysis *C. oxyrinchus* must be considered globally extinct, as there is no record after 1940 and no trace of its survival can be found. Now, the only known autochthonous *Coregonus* in the North Sea basin are found in the River Vida (Denmark) and genetic analyses have shown them to be *C. maraena* (Hansen *et al.*, 1999), as do the present results. Because the present study indicates *C. oxyrinchus* is extinct, restocking programmes based on the transfer of fishes from the River Vida to other rivers (England, Rhine, Meuse and Schelde) is counterproductive to effective conservation and management of natural resources, resulting only in the introduction of an exotic species (*C. maraena*) into drainages outside its native range.

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APPENDIX. Material examined

Coregonus oxyrinchus: BMNH 1844.11.11.15, 1 ex., 228 mm L_S ; Netherlands: Gray, E. J. E.; 1844. BMNH 1862.11.20.1, neotype, 306 mm L_S ; Belgium: Prov. Antwerp: Antwerp, River Schelde; van Voorst J.; 1862. BMNH not catalogued, 148.5 mm L_S ; England: South Coast of England; F. Day Esq. NMBE 1020331–1020332, 2 ex., 241–279 mm L_S ; Netherlands: Prov. Zuid-Holland: River Lek at Rotterdam; 20 Mar. 1906. MNHN 0000–2786, 1 ex., 326 mm L_S ; France: River Meuse; Milbert, 1856. MNHN B-2497, 1 ex., 279 mm L_S ; Netherlands: Prov. Noord-Holland: Haarlem: River Rhine; Temminck. MNHN 0000–1502, 1 ex., 131 mm L_S ; Netherlands: Prov. Noord-Holland: Haarlem, Amsterdam: River Rhine; Valenciennes. ZSM 4898, 1 ex., 267 mm L_S ; Netherlands: River Meuse; 25 Apr 1855. ZMA 108.138, 1 ex., 175 mm L_S ; Netherlands: Prov. Noord-Holland: Amsterdam: Entrepot Dok; Aug 1896. ZMA 123.601, 2 ex., 218–227 mm L_S ; Netherlands: River Meuse; Fauna Collection Natura Artis Magistra; 1884. ZMA 123.602, 3 ex., 164–248 mm L_S ; Netherlands: Prov. Zuid-Holland/Noord-Brabant: Hollandsch Diep; 1886. ZSM 25478, 2 ex., head only, 76–80 mm L_H ; Netherlands: Rhein; A. Thienemann, 1935. *Coregonus maraena*: ZMB 11786, 2 ex., 140–155 mm L_S ; Germany: Prov. Niedersachsen: River Ems; 22 Oct 1881. ZMB 23404, 2 ex., 421–449 mm L_S ; Poland: Prov. Województwo Zachodniopomorskie: Lake Miedwie; 7 Mar 1905. ZMB 3759, 1 ex., 328 mm L_S ; Germany: Prov. Hamburg: River Elbe; 1860. MNHN B-2493, 1 ex., 408 mm L_S ; Germany: Prov. Brandenburg: Berlin: River Spree at Berlin, Elbe basin; A. v. Humboldt, 1830. NMW 92957, 1 ex., 218 mm L_S ; Denmark: Prov. Jütland; Krøyer, 5 Jun 1845. ZMA 121.721, 1 ex., 244 mm L_S ; Netherlands: Prov. Friesland: IJsselmeer at Kornwerd; W. Dekker & J. van Willigen, 13 Jul 1997. ZMA 121.720, 1 ex., 203 mm L_S ; Netherlands: Prov. Noord-Holland: Breezand; W. Dekker & J. van Willigen, 21 Jul 1997. ZMA 121.723, 2 ex., 151–197 mm L_S ; Netherlands: Prov. Zuid-Holland: Haringvliet; Haringvliet; H. Nijssen, Dec 1996. GNM Pi. Su. 65, 2 ex., 203–210 mm L_S ; Sweden: Prov. Västra Götaland: Göta älv at Göteborg; A. Malmgren, 3 Jul 1849. GNM Pi. Su. 1838, 1 ex., 305 mm L_S ; Sweden: Prov. Västra Götaland: Vänern Källandsö; 2 Apr 1838. GNM Pi. Su. 2369, 1 ex., 148 mm L_S ; Sweden: Prov. Västra Götaland: Göta älv at Alelyckan; Nov 1933. ZMUC 3, 1 ex., 299 mm L_S ; Denmark: Jütland: Prov. Ringkøbing: Ringkøbing Fjord. ZMUC 8 – 9, 2 ex., 250–268 mm L_S ; Denmark: Jütland: Prov. Ribe: Ribe Å; 1879. ZMUC 10 + 12–13, 3 ex., 169–179 mm L_S ; Denmark: Prov. Nordjylland: Vesterhavet: Nordsøen (North Sea); 1890. ZMUC 15, 1 ex., 209 mm L_S ; Denmark: Prov. Ribe: Ribe Å. ZMUC P1934, 1 ex., 311 mm L_S ; Denmark: Prov. Ribe: Ribe Å. ZMUC P19521, 1 ex., 268 mm L_S ; Denmark: Prov. Nordjylland/Viborg: Limfjorden (Limfjord); 1835. FSJF 517, 20 ex., 235–372 mm L_S ; Netherlands: Prov. Noord-Holland/Friesland/Flevoland: IJsselmeer; RIVO, 2000/2001. FSJF 518, 20 ex., 141–447 mm L_S ; Germany: Schleswig-Holstein: lower River Treene, a tributary to River Eider; J. Freyhof, Dec. 2000. FSJF 519, 15 ex., 320–401 mm L_S ; Germany: Schleswig-Holstein: River Schlei; J. Freyhof, Dec. 2000. FSJF 520, 18 ex., 342–495 mm L_S ; Germany: Mecklenburg-Vorpommern: estuary of River Peene; J. Freyhof, Dec. 2000. FSJF 521, 17 ex., 280–435 mm L_S ; Germany: Brandenburg: River Odra at Schwedt; J. Freyhof, Nov. 2000. ZMB 23396, 3 ex., 137–165 mm L_S ; Germany: Niedersachsen: Emden: River Ems; 1866.

ZMB 11786, 2 ex., 141–144 mm L_S ; Germany: Niedersachsen: River Ems; 1881. *Coregonus widegrenii*: FSJF 524, 4 ex., 369–439 mm L_S ; Germany: Prov. Schleswig-Holstein: River Schlei; J. Freyhof, Dec. 2000. FSJF 525, 3 ex., 354–404 mm L_S ; Deutschland: Prov. Mecklenburg-Vorpommern: estuary of River Peene; J. Freyhof, Dec. 2000. FSJF 226, 10 ex., 360–410 mm L_S ; Deutschland: Prov. Mecklenburg-Vorpommern: DREWITZER See; J. Freyhof, 15 Dec. 2003. *Coregonus* sp. 'Rhine': ZMA 114.450, 1 ex., 196 mm L_S ; Netherlands: Prov. Gelderland: cooling water of the Nijmegen nuclear power station at River Waal; R. H. Haddingh, 8 Jan. 1981. ZMA 115.389, 4 ex., 150–205 mm L_S ; Netherlands: Prov. Noord-Brabant: Hollands Diep at Moerdijkbrug; W. Klop, Nov. 1978/Mar 1979. ZMA 116.723, 1 ex., 150 mm L_S ; Netherlands: Prov. Noord-Holland/Friesland/Flevoland: IJsselmeer at de Kreupel; R. H. Haddingh, 28 Jul 1981. ZMA 121.092, 1 ex., 257 mm L_S ; Netherlands: Prov. Zuid-Holland/Noord-Brabant: Biesbosch-Nationalpark at Merwede/Amer; Klop, Mar 1992. ZMA 121.093, 1 ex., 278 mm L_S ; Netherlands: Prov. Gelderland/Utrecht/Zuid-Holland: River Lek; Bunt, 12 Feb. 1992. ZMA 120.607, 4 ex., 207–255 mm L_S ; Netherlands: Prov. Gelderland: River Rhine at Spijk (Lobith), close to German border; A. v. Sonsbeek, Nov 1988. ZMA 112.784, 1 ex., 181 mm L_S ; Netherlands: Prov. Zuid-Holland: River Lek at Bergambacht, R. Boddeke, Dec 1967.

L_S , standard length; L_H , head length.