

Crossbill (Genus *Loxia*) evolution in the West Palearctic - a look at the fossil evidence

TOMMY TYRBERG

Abstract

The systematics of West Palearctic crossbills of Genus *Loxia* has long been disputed. The Scottish form *scotica* has been considered a species or a subspecies of either *Loxia curvirostra* or *L. pytyopsittacus*. The reason is the size and form of its bill which is intermediate between that of the two species. It feeds on pine cones as do four Mediterranean subspecies which also have larger bills than spruce feeding *curvirostra*. An examination of about 30 fossil *Loxia* records reveals that *curvirostra* type crossbills lived in South Europe and the Near East all through the last glaciation and that *pytyopsittacus* type crossbills lived in the Alps towards the end of the glaciation. These South European crossbills must have fed on Pine since no other conifers were available, and they must have been isolated from Siberian congeners. With the spread of Pines northwards with the retreat of the ice the crossbills followed.

The fossils allow two alternative hypothesis depending on whether the large crossbills in the Alps are considered a species or not. If they were *pytyopsittacus* this species is rather old and both *curvirostra* and *pytyopsittacus* spread northwards at the end of the glaciation. One of the species must have gone extinct in Scotland and South Europe and possible *curvirostra* must have merged with *curvirostra* spreading with the Spruce from the east. On the other hand, if the Mediterranean crossbills of the Ice Age represent a single, variable species then all the large-billed forms, *pytyopsittacus*, *scotica* and the Mediterranean subspecies are descendants of the old "Pine" crossbills of South Europe.

Tommy Tyrberg, Kimstadvägen 37, S-610 20 Kimstad, Sweden

The taxonomy of crossbills (Genus *Loxia*) in the West Palearctic has frequently been disputed. The most commonly held view is that two species exist, the monotypic Parrot Crossbill *Loxia pytyopsittacus* in boreal pine forests in Fennoscandia and northwestern Russia and the polytypic Common Crossbill *Loxia curvirostra* mainly in spruce forests almost throughout the West Palearctic.

The development of the bill, and to some extent speciation, among crossbills seems to depend largely on the size and hardness of the cones used for food (e.g. Lack 1944, Newton 1967, Benkman 1987a, b, 1989). The Parrot Crossbill with its heavy bill specializes in pine cones, the Common Crossbill in the less refractory cones of Spruce *Picea* spp. and the even thinner-billed Two-barred Crossbill *Loxia leucoptera* in cones of Larch *Larix* spp.

This seemingly clearcut picture is however complicated by the large intraspecific variation in bill size in *L. curvirostra* as this species is usually understood. This is especially true of *L. (curvirostra) scotica* which is confined to the relict Scots Pine forests of the

Scottish Highlands (Nethersole-Thompson 1975, Sharrock 1976).

Being specialized in feeding on pine cones *scotica* crossbills have nearly as heavy bills as *pytyopsittacus*, and they have sometimes been considered a subspecies of *pytyopsittacus* (e.g. by Hartert & Steinbacher (1932) and Nethersole-Thompson (1975)) or as a separate species *L. scotica* (e.g. Knox 1975, 1990, Voous 1978).

Four other heavy-billed subspecies feeding on pine cones exist in the Mediterranean Basin, *corsicana* on Corsica, *balearica* on the Balearics, *poliogyne* in the Atlas Mountains and *guillemardi* on Cyprus. These populations might well have equivalent taxonomic status to *scotica* but are usually considered to be subspecies of *curvirostra* though the reasons for this view given by Massa (1987) and Knox (1990) are not very convincing.

Nethersole-Thompson (1975) and Murray (1978) have proposed a scenario for the evolution of West Palearctic crossbills. They suggest that a population of *curvirostra* became isolated in western Europe during the last (Würmian) glaciation. During the climax of

this glaciation the Spruce was extinct west of the Urals, except for small relict stands in parts of the Balkans (e.g. Huntley & Birks 1983), and the isolated crossbills evolved to become heavy-billed pine cone specialists. At the end of the glaciation these crossbills followed the pine forests northwards into Britain and Fennoscandia where they evolved into *scotica* and *pytyopsittacus*, respectively.

Later, during the Holocene, Spruce forests (and *curvirostra* crossbills) expanded westwards from the Urals. The larger size and somewhat different vocalizations of *pytyopsittacus* compared to *scotica* may then have come about through character displacement when *pytyopsittacus* and *curvirostra* became sympatric.

Knox (1990) on the other hand suggests that each of the heavybilled crossbill populations has evolved independently in their present ranges: the Mediterranean populations from irrupting *curvirostra* (presumably during the Holocene) and *scotica* from birds isolated during the last glacial maximum in hypothetical relict Scots Pine forests on the exposed continental shelf northwest of Scotland and/or southwest of Ireland.

This postulated refuge for crossbills west of the British isles during the glacial maximum (Huntley 1988, Knox 1990) must however be considered very questionable. Certainly "...survival of relatively thermophilous trees and associated species in a probably narrow zone of oceanic vegetation" (Huntley 1988) is extremely unlikely. During the glacial maximum the North Atlantic was an arctic sea and in arctic and subarctic areas the wind-exposed and ice-bound coasts are invariably bleak and treeless while the richest vegetation (including forest outposts) is found at protected sites well inland. Even if relict stands of Scots Pine did survive somewhere to the west of the British Isles it seems very unlikely that they would consistently have produced sufficient seed-crops to sustain a viable crossbill population. It should be noted that plants (but not birds) can survive for protracted periods in quite small enclaves with exceptionally favourable microclimate and that Pine seed production is extremely irregular at the northern edge of the species' range.

Which hypothesis about crossbill evolution is correct may ultimately be determined through DNA analysis since this reveals branching patterns and genetic distances between populations. However, the status of the different populations may remain doubtful even then since it is far from clear how genetic differences translate into taxonomic categories.

The fossil record of crossbills

There is however a more direct way to study the past history of West Palearctic crossbills through fossils. It

is perhaps not generally realized how good the Pleistocene avian fossil record is in the West Palearctic. Information is available from well over 1000 sites, and virtually every extant West Palearctic bird is also known in the fossil record. Crossbills are quite rare as fossils, but have nevertheless been recorded from some 30 sites in the West Palearctic.

A problem when evaluating crossbill fossils is that, while the genus *Loxia* is morphologically rather distinct, at least postcranial bones of *curvirostra* and *pytyopsittacus* can currently only be distinguished by size. A record of *pytyopsittacus* therefore really means "a *pytyopsittacus* sized Crossbill", not necessarily a bird belonging to the species *pytyopsittacus* as this is currently understood. On the other hand *L. leucoptera* can be morphologically distinguished by skeletal characters at least in some cases according to Cassoli (1980).

The Middle Pleistocene record

The oldest crossbill record is of *cf Loxia curvirostra* from Stránská Skála in Czechoslovakia (Jánossy 1972). The main interest of this record is that it shows that *curvirostra*-sized crossbills were already present in Europe during the early part of the Middle Pleistocene.

The other two Middle Pleistocene finds can both be dated with fair certainty to the penultimate glaciation (= Isotope Stage 6 c. 130 000-200 000 BP). One is *L. cf curvirostra* from the Glutton stratum in Tornewton Cave (Devonshire, England) (Harrison 1980, 1987). The other find is from Grotte de Lazaret (Alpes Maritimes, France) and has interestingly been determined as *pytyopsittacus* (Mourer-Chauviré 1975). A third record which may also be Late Middle Pleistocene is *curvirostra* from Fontéchevade (Charente, France) (Mourer-Chauviré 1975). This site is conventionally dated to the Eemian interglacial (= Isotope stage 5e 117 000-127 000 BP). Both the mammalian microfauna and the avifauna however indicates that it must be either from the very end of the penultimate glaciation or from a still cool initial phase of the interglacial, so this record is best treated together with the previous two.

These three records indicate that both *curvirostra*-sized and *pytyopsittacus*-sized crossbills were present in western Europe during the penultimate glaciation, but whether they belonged to two different species or a single polytypic species is uncertain. The faunas at all three sites indicate cooler and drier climate than today, but not extreme glacial conditions.

Late Pleistocene crossbills

Eem Interglacial - Early Würm

There are no records of crossbills from the Eemian interglacial (Isotope Stage 5e 127 000-117 000 BP).



Fig. 1. Sites where crossbill *Loxia* fossils have been found in the West Palearctic. Shaded areas indicate areas with high frequency of *Pinus* pollen at the beginning of the Late Glacial c. 13 000 BP (Huntley & Birks 1983).

Fyndplatser för korsnäbbsfossil i Västpalearktis. Skuggade fält markerar områden med hög tallpollenfrekvens ca 13 000 BP (Huntley & Birks 1983).

Key to sites Nyckel till lokaler:

Middle Pleistocene: 1. Stránská Skála, 2. Tornewton cave, 3. Grotte de Lazaret, 4. Fontéchevade.

Late Pleistocene: 5. Bacho Kiro, 6. Istallóskő, 7. Sandalja II, 8. Herman Otto Cave, 9. Ossiferous Fissure C8, 10. Syuren I, 11. Pilisszántó 1, 12. Salpêtrière à Remoulins, 13. Arene Candide, 14. Puskaporos, 15. Merlin's Cave, 16. Pinhole Cave, 17. Derbyshire Peak, 18. Grotte de Massat, 19. Remetehgy, 20. Hayonim Cave, 21. Grotta Romanelli, 22. Rislisberghöhle.

Uncertain Date: 23. Cova Nova, 24. Balcárka, 25. Certova Díra, 26. Jirická Skála, 27. Zechovice II, 28. Caverna dei Verezzi, 29. Grotta dei Fanciulli, 30. San Cosimato, 31. Gudenushöhle, 32. Merkenstein.

This is not surprising since interglacial avifaunas are quite rare. It is more surprising that crossbill fossils from the early part of the last glacial cycle (Isotope stages 4-5d c. 60 000-115 000 BP) are quite rare.

The only find which can definitely be assigned to this interval is a *curvirostra* from layer 13 in Bacho Kiro Cave in Bulgaria (Bochenski 1982). This layer has been tentatively correlated with the Eleutheropolis

interstadial (probably =Isotope Stage 5a, ca 80 000 BP) (Kozłowski et al. 1982). During this relatively mild interstadial spruce (*Picea abies* and the extinct *Picea omoricoides*) were apparently common and widespread in Europe (e.g. Nilsson 1972).

The scarcity of records from the early Würmian is strange. Though sites of this age are considerably less common than those of Middle or Late Würmian age, there are several rich faunas in which crossbills might be expected to occur.

Mid Würmian

During the "Mid-Würmian interstadial complex" (Isotope Stage 3 c. 60 000-25 000 BP) crossbill records become somewhat more numerous. Sites definitely from this interval include Istallóskő in Hungary (Jánossy 1955, 1986) and Sandalja II (layer H) in Yugoslavia (Malez-Bacic 1979, Malez 1988). More uncertainly dated sites which may also belong to this interval include Herman Otto Cave in Hungary (Lambrecht 1915), Ossiferous Fissure C8 at Creswell Crags in England (Jenkinson 1984), and Syuren I in Crimea (Tugarinov 1937, Voinstvenskij 1963, 1967). All these Middle Würmian finds have been attributed to *curvirostra*.

The late Würmian Glacial Maximum

The Würmian Glacial maximum comprises approximately the period 25 000-13 000 BP with a "hard core" of maximum glaciation c. 22 000-17 000 BP. Sites with crossbills from this period include Pilisszántó 1 in Hungary (*curvirostra*) (Jánossy 1986, Lambrecht 1915) Salpêtrière à Remoulins in France (*pytyopsittacus*) (Vilette 1983, 1984) and the lower layers (P4-P10) at Arene Candide in Italy (*curvirostra* and *pytyopsittacus*) (Cassoli 1980). Puskaporos in Hungary (*curvirostra*) (Lambrecht 1916, 1933) may also belong to this interval.

The most interesting of these sites is Salpêtrière à Remoulins both because of the possible presence of *pytyopsittacus* and because the layer where the crossbill occurs (30Ab/A) has been ¹⁴C-dated to 20 630±770 BP (Vilette 1983), i.e. very close to the glacial maximum. The oldest records from Arene Candide probably also date from close to the glacial maximum.

The Late Glacial

The Late Glacial spans approximately the last three millennia of the Würmian glaciation, c. 13 000-10 000 BP. Crossbill localities from this period are: Merlin's Cave, Pinhole Cave (layers 3-4) and caves in the Derbyshire Peak District in England (*curvirostra*) (Bate 1901, Bramwell 1975, Harrison 1980, 1987, Jenkinson 1984), Grotte de Massat in France (*curvirostra*) (Milne-Edwards 1875, Clot & Mourer-Chauviré 1986),

Remetehegy in Hungary (*curvirostra*) (Lambrecht 1933, Jánossy 1986), Hayonim cave in Israel (*curvirostra*) (Tchernov 1979), Arene Candide (layers M3, P1-2) (*curvirostra*, *pytyopsittacus* and *leucoptera*) and Grotta Romanelli (*curvirostra*) in Italy (Cassoli et al. 1979, Cassoli 1980), Rislisberghöhle in Switzerland (*Loxia* sp.) (Lepiksaar 1983) and Sandalja II (layer B) in Yugoslavia (*curvirostra*) (Malez-Bacic 1979, Malez 1988). The record from Israel is well south of the present range of any crossbill, but forests, with Aleppo Pine *Pinus halepensis*, were considerably more widespread in Israel during the last glaciation than today (Horowitz 1979), and it is quite likely that a breeding population existed at that time in the mountains of the Levant.

Discussion

The fossils prove that crossbills of *curvirostra* size were definitely present in southern Europe and the Near East at least from the middle Würmian onwards and probably throughout the Würmian, and that larger birds, of *pytyopsittacus* size, existed at least in a limited area in the Western Alps from the glacial maximum onwards.

To what extent these south European crossbills were isolated from their Siberian congeners during the early and middle Würmian is uncertain. Much of eastern Europe was probably forest steppe with at least some conifers during most of this interval. During the glacial maximum, say from 25 000 BP to 13 000 BP, isolation was probably complete. Most of central and eastern Europe north and east of the Carpathians was a treeless steppe tundra during that interval. Conditions in the southern Balkans, Anatolia, Caucasus and the Near East were cool and arid with forest areas greatly reduced and vast areas of *Artemisia*-dominated dry steppe. Whether an isolation period of approximately 10 000 years is sufficient for speciation to take place is uncertain. Several bird populations in the West Palearctic have been isolated for approximately this period since the end of the last glaciation without speciating, though some may be close to species status (e.g. Tyrberg 1991).

At least during the latter half of the Würmian the south European crossbills must have fed mainly on pine cones since other conifers were either absent or rare west of the Urals at least after the middle Würmian (Huntley & Birks 1983). The dependence on pines is supported by a palaeoecological analysis of the Late Glacial Grotta Romanelli avifauna (Cassoli et al. 1979) which indicates that the crossbills there were probably living in stands of *Pinus sylvestris* and *Pinus montana* growing in microclimatically favourable sites along the coastal cliffline in Apulia. Unfortunately Grotta Romanelli is the only Pleistocene crossbill site for which such an analysis is available.

It seems likely that these crossbills would have evolved a heavy "pine-cone breaking" bill, and would therefore be most similar to *scotica* or the heavy-billed Mediterranean subspecies. This is at least partly confirmed by a record from Cova Nova on Mallorca, unfortunately only loosely dated as late Pleistocene, of a crossbill with a mandible intermediate between *curvirostra* and *pytyopsittacus* (Florit & Alcover 1987).

Loxia leucoptera

Loxia leucoptera is a well differentiated form. It is probably a fairly old species and most likely originated outside Europe, either in the East Palearctic or the Nearctic. Interestingly, even this thin-billed species has developed a southern isolate with a heavy bill adapted to pine cones, *Loxia leucoptera megaplaga*, in the montane pine forests of Hispaniola. This species may never have been a regular breeder in most of Europe since it is adapted to the cones of Larch *Larix* spp.

The only fossil record is of two individuals from layer P1 in the Arene Candide cave on the Italian Riviera (Cassoli 1980). These are dated to the late glacial, perhaps the Bölling Interstadial (c. 12-13 000 BP).

The closest Siberian taiga suitable for *leucoptera* was probably to be found in the southern Urals at that time and it is possible that the Arene Candide finds are from birds irrupting from there. Today such irruptions usually end up in Fennoscandia, but during the Late Glacial the Scandinavian icecap presumably would have deflected the birds to the south into central or southern Europe.

It is however possible that *leucoptera* bred for awhile in the Alps during the Late Glacial and the Early Holocene. *Larix decidua* survived the glacial maximum in the Alps and on a smaller scale in the northern Carpathians. A rather short-lived expansion of the Larch in the Alps near the Pleistocene/Holocene border (Huntley & Birks 1983) may for a while have made it possible for a resident population of *leucoptera* to exist in the Alps. A modern analogue would be the small breeding population of Siberian Nutcrackers *Nucifraga caryocatactes macrorhynchos*, a Cembra Pine specialist, which have persisted for more than a decade in northern Sweden after an irruption, at least partly sustained by introduced Cembra Pines (e.g. Elmberg & Mo 1984).

The Larch may have been widely distributed in Europe during the two latest interglacials and during early Würmian interstadials (Huntley & Birks 1983, Nilsson 1972). There is however no evidence of *leucoptera* at that time.

Phylogenetic hypotheses

The fossil record is unfortunately insufficient to give an unequivocal picture of crossbill speciation. Instead

two alternative phylogenies of West Palearctic crossbills can be constructed based on the fossil evidence, depending on whether the records of *pytyopsittacus* are accepted at face value or not. If the records are really of the extant species, then *pytyopsittacus* is a fairly old form, dating at least from the late Middle Pleistocene (as evidenced by the record from Lazaret). This implies that *pytyopsittacus* and *curvirostra* managed to coexist in the limited areas of pine forest in southern Europe during the glacial maximum. This is perhaps rather unlikely since the several extant cases of isolated crossbill populations each involve only one of the extant species. The counterexample from Newfoundland where both *curvirostra* and *leucoptera* exist is only apparent since *leucoptera* is apparently not resident, but move in and out of the island depending on the cone crop (Benkman 1989).

On the other hand all the Riss-Würmian crossbills in southern Europe may have belonged to a single rather variable species. It is certainly suggestive that all the records of *pytyopsittacus* are from a limited area in the Western Alps and may represent a large-bodied local population in that area.

The two hypotheses outlined above imply different scenarios to explain the extant distribution of crossbill subspecies in the West Palearctic.

Scenario A (Two late Pleistocene species)

At the end of the glaciation both species presumably followed the expanding pine forests northwards (that crossbills did move north at this time is shown by the English and Swiss records from areas where crossbills couldn't possibly have occurred during the glacial maximum). In this scenario *pytyopsittacus* ended up isolated in Fennoscandia presumably together with a population of *curvirostra* of southern derivation when pine forests largely disappeared from the European mainland north of the Mediterranean about 7 000-8 000 BP (Huntley & Birks 1983). Only one species survived in the relict pine forests of Scotland which is not surprising considering their limited distribution. Later, from the Mid-Holocene onwards spruce-adapted *c. curvirostra* expanded westwards from the Urals together with *Picea* and interbred with any large-billed *curvirostra* crossbills remaining in Fennoscandia or on the European mainland. The *scotica* crossbills were not affected due to their isolation (until forestry plantations started during the nineteenth century there were no coniferous forests closer to Scotland than in southern Norway and the mountains of central Europe).

The large-billed crossbills on the Mediterranean Islands and in Maghreb in North Africa are probably direct descendants of Pleistocene populations which

have avoided being displaced or swamped by smaller-billed "Spruce crossbills" in their somewhat isolated ranges where pines are moreover the dominant conifers. It certainly does not seem likely that these races have differentiated from "Spruce crossbills" during the Holocene as suggested by Harrison (1982) since this would imply that the large-billed crossbills which certainly existed at least on Mallorca during the late Pleistocene either died out or were displaced by smaller-billed birds which then once again developed larger bills. The presence of only one of the two Pleistocene species in the Mediterranean area must be ascribed to the same factors as in Scotland, namely that one species has become extinct during the Holocene in the rather circumscribed areas of suitable habitat.

Scenario B (*One variable species*)

This scenario is considerably simpler, and is practically identical to the views of Murray (1978). The Pleistocene Mediterranean crossbills simply followed the pine forests northwards and became isolated in Fennoscandia and Scotland. Later *c. curvirostra* expanded westwards together with the Spruce and caused *pytyopsittacus* to diverge somewhat through character displacement. Any remaining "Pine crossbills" on the European mainland were displaced by *c. curvirostra* while the Mediterranean and Scottish forms persisted, though there may have been some intergradation. In Fennoscandia hybridization between *curvirostra* and *pytyopsittacus* seems to be quite rare and according to Knox (1990) the same is true for *curvirostra* and *scotica* in Scotland.

These two scenarios are in principle testable by chemotaxonomic methods. If scenario A is true then *pytyopsittacus* should be well separated from all other West Palearctic crossbills (except perhaps *scotica*), while the large-billed Mediterranean forms should be rather more distant from *c. curvirostra* than from each other.

If Scenario B is true, then *pytyopsittacus*, *scotica* and the large-billed Mediterranean forms should all be fairly closely related to each other while *c. curvirostra* should be more distant.

References

- Bate, D. 1901. A short Account of a Bone Cave in the Carboniferous Limestone of the Wye Valley. *Geol. Mag.* 8:101-106.
- Benkman, C.W. 1987a. Food profitability and foraging ecology of crossbills. *Ecol. Monogr.* 57:251-267.
- Benkman, C.W. 1987b. Crossbill foraging behavior, bill structure and patterns of food profitability. *Wilson Bull.* 99:351-368.
- Benkman, C.W. 1989. On the Evolution and Ecology of Island populations of Crossbills. *Evolution* 43(6):1324-1330.
- Bochenki, Z. 1982. Aves. In Kozłowski, J.K. (ed.): *Excavation in the Bacho Kiro Cave (Bulgaria). Final Report*, Pp. 31-38. Warszawa.
- Bramwell, D. 1977. Archaeology and Palaeontology. In Ford, T.D. (ed.): *Limestones and Caves of the Peak District*. Pp. 263-292. Norwich.
- Cassoli, P.F. 1980. L'Avifauna de pleistocene superiore delle Arene Candide (Liguria). *Memorie dell'Istituto Italiano di Paleontologia Umana* N. S. 3:155-234.
- Cassoli, P.F., Segre, A.G. & Segre, E. 1979. Evolution morphologique et écologique de la côte de Castro (Pouilles) dans les Pléistocène final. In Sonnevile-Bordes, D. (ed.): *La fin des temps glaciaires en Europe. Colloques Internationaux de CNRS* N:o 271:325-332.
- Clot, A. & Mourer-Chauviré, C. 1986. Inventaire systematique des oiseaux quaternaires des Pyrenées Françaises. *Munibe* 38:171-184.
- Elmberg, J. & Mo, A. 1984. Smalnäbbad nötkråka *Nucifraga caryocatactes macrorhynchos* - nyetablerad häckfågel i Västerbotten. *Vår Fågelvärld* 43:193-197.
- Florit, X. & Alcover, J. A. 1987. Els ocells del pleistocè superior de la Cova Nova (Capdepera, Mallorca) I-II. *Bolleti de la societad d'Historia Natural de les Balears* 31:7-44.
- Harrison, C.J.O. 1980. Pleistocene bird remains from Tornewton Cave and the Brixham Windmill Hill Cave in south Devon. *Bull. Br. Mus. nat. Hist. (geol.)* 33(2):91-100.
- Harrison, C.J.O. 1982. *An Atlas of the Birds of the Western Palearctic*. London
- Harrison, C.J.O. 1987. Pleistocene and Prehistoric Birds of South-West Britain. *Proc. Univ. Bristol Spelaeol. Soc.* 18 (1):81-104.
- Hartert, E. & Steinbacher, F. 1932. *Die Vögel der Paläarktischen Fauna*. Ergänzungsband, Heft 1. Berlin.
- Horowitz, A. 1979. *The Quaternary of Israel*. New York.
- Huntley, B. 1988. European post-glacial vegetation history: a new perspective. *Proc. Int. Orn. Congr.* XIX:1061-1077.
- Huntley, B. & Birks, H. J. B. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0-13,000 Years Ago*. Cambridge.
- Jánossy, D. 1955. Die Vogel- und Säugetierreste der spätpleistozänen Schichten der Höhle von Istállóskő. *Acta Arch. Acad. Sci. Hung.* 5:149-181.
- Jánossy, D. 1972. Die mittelpleistozäne Vogelfauna der Stránská Skála. *Anthropos (Brno)* 20 (N. S. 12):35-64.
- Jánossy, D. 1986. *Pleistocene Vertebrate Faunas of Hungary*. Developments in Palaeontology and Stratigraphy 8. Amsterdam.
- Jenkinson, R.D.S. 1984. Creswell Crags. Late Pleistocene Sites in the East Midlands. *BAR British Series* 122.
- Knox, A.G. 1975. Crossbill Taxonomy. In Nethersole-Thompson, S.D. *Pine Crossbills*. Pp. 191-201. London.
- Knox, A.G. 1990. The sympatric breeding of Common and Scottish Crossbills *Loxia curvirostra* and *L. scotica* and the evolution of crossbills. *Ibis* 132:454-466.
- Kozłowski, J.K. (ed.) 1982. *Excavation in the Bacho Kiro Cave Bulgaria. Final Report*. Warszawa.
- Lack, D. 1944. Ecological aspects of species-formation in passerine birds. *Ibis* 86:260-286.
- Lambrecht, K. 1912. Fossile Vögel des Borsoder Bükk-Gebirges. *Aquila* 19:270-288.

- Lambrecht, K. 1915. Die Vögel der Felsnische Pilisszántó. *Mitt. a. d. Jahrb. Kgl. Ung. Geol. Reichsanst.* 23:477-517.
- Lambrecht, K. 1916. Die pleistozäne und prähistorische Vogelfauna der Felsnische am Remetehegy. *Mitt. a. d. Jahrb. Kgl. Ung. Geol. Reichsanst.* 22:390-404.
- Lambrecht, K. 1933. *Handbuch der Paläornithologie*. Berlin.
- Lepiksaar, J. 1983. Die Vögel und die Fische. In Stampfli, H-R: *Risli-berghöhle*:83-125. Bern.
- Malez, V. 1986. Novi prilog poznavanju gornjopleistocenske ornitofaune iz Sandalje kod Pule u Istri (Hrvatska, Jugoslavija). *RAD JAZU Knj.* 424:129-151.
- Malez-Bacic, V. 1979. Pleistocenska ornitofauna iz Sandalje u Istri te njezino stratigrafsko i paleoekolosko znacenje. *Paleontologica Jugoslavica* 21:1-46.
- Massa, B. 1987. Variation in Mediterranean crossbills *Loxia curvirostra*. *Bull. Brit. Ornithol. Club* 107:118-129.
- Milne-Edwards, A. 1875. Observations sur les oiseaux dont les ossements ont été trouvés dans les cavernes du Sud-Ouest de la France. *Materiaux pour l'hist. primit. et naturelle de l'homme Sér. 2*, Tom. 6:473-503 (not seen).
- Mourer-Chauviré, C. 1975. *Les oiseaux du pléistocène moyen et supérieur de France*, 1-2 fasc. Thèse de l'Université Claude Bernard - Lyon.
- Murray, R.D. 1978. Crossbill evolution. *Br. Birds* 71:318-319.
- Nethersole-Thompson, D. 1975. *Pine Crossbills*. London.
- Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis* 109:33-98.
- Nilsson, T. 1972. *Pleistocen*. Lund.
- Sharrock, J.T.R. 1976. *The Atlas of Breeding Birds in Britain and Ireland*. Tring.
- Tchernov, E. 1979. Quaternary Fauna. In Horowitz, A: *The Quaternary of Israel*. Pp. 259-290. New York.
- Tugarinov, A. Ya. 1937. [Die Vögel der Krim aus der Zeit der Würmvereisung.] *INQUA Soviet sect.* 1:97-114.
- Tyrberg, T. 1991. Arctic, Montane and Steppe Birds as Glacial Relicts in the West Palearctic. *Verh. orn. Ges. Bayern*: 25:29-49.
- Vilette, P. 1983. Avifaunes du Pléistocène final et de l'holocène dans le Sud de la France et en Catalogne. *Atacina* 11:1-190.
- Vilette, P. 1984. Quelques données sur les avifaunes du Languedoc méditerranéen (sud de la France) de la fin du pleistocène et de l'holocène. *Cahiers Ligures de Préhistoire et de Protohistoire*. N. S. 1:198-210.
- Voinstvenskij, N.A. 1963. Deyak risi skhasnoi ornitofauna Krimy ta ii istoriya protyagom antropogeny. In *Nazemni chrebetni Ukrainy*. Pp 51-63. Kiev.
- Voinstvenskij, N.A. 1967. Iskopaemaya Ornitofauna Ukrainy. *Prirodnaya Obstanovka i Fauny Prozhlovo* 3. Naukova Dumka, Kiev, p. 3-76.
- Voous, K.H. 1978. The Scottish Crossbill: *Loxia scotica*. *Br. Birds*. 71:3-10.

Sammanfattning

Artbildning hos korsnäbbar (släktet Loxia) i Västpalearktis — en studie av fossila fynd.

Systematiken hos de västpalearktiska korsnäbbarna har länge varit omstridd. Framst har oenigheten gällt den skotska

korsnäbbens status. Den har ömsom räknats som en ras av mindre korsnäbb, en ras av större korsnäbb eller en egen art, *Loxia scotica*.

Orsaken till osäkerheten är främst att den skotska korsnäbben i viktiga avseenden, bl a näbbens storlek och form, är intermediär mellan större och mindre korsnäbben.

Korsnäbbarnas näbbstorlek styrs främst av deras födoval, d.v.s. hur pass hållfasta de kottar är som korsnäbbarna måste forcera för att komma åt sin huvudföda, barrträdsfrön.

Den stornäbbade större korsnäbben lever främst på tallfrö, den mindre korsnäbben på granfrö och bändelkorsnäbben på lärkträdsfrö. Den skotska korsnäbben och fyra korsnäbbspopulationer i medelhavsområdet (*corsicana* på Korsika, *balearica* på Balearerna, *poliogyra* i Atlasbergen och *guillemardi* på Cypern) lever främst på tallfrö och har följdriktigt kraftigare näbbar än den mindre korsnäbbens nominatras *Loxia c. curvirostra*.

Flera teorier har framförts framförallt för att förklara uppkomsten av de skotska korsnäbbarna. Enligt en teori (t.ex. Nethersole-Thompson 1975) härstammar både den större korsnäbben och den skotska korsnäbben från en korsnäbbspopulation som isolerades i tallskogsområden i Sydvästeuropa under den senaste istiden. Efter istidens slut följde korsnäbbarna tallskogarna norrut och isolerades genom Nordsjöns uppkomst i två populationer. Senare invandrade den mindre korsnäbben österifrån tillsammans med granen och orsakade en viss förskjutning hos den större korsnäbbens egenskaper genom "character displacement".

En annan teori hävdas av bl. a. Knox (1975, 1990), nämligen att den skotska korsnäbben uppstod under den senaste istiden i hypotetiska relikta tallskogar på kontinentalsockeln väster om de Brittiska öarna.

En källa som hittills knappast använts för att klarlägga korsnäbbarnas historia är fossilfynden. Inalles har korsnäbbar anträffats på mer än 30 platser i Västpalearktis (Fig. 1). Ett problem vid bedömningen av fossilfynden är dock att skelett av större och mindre korsnäbb endast kan skiljas på storleken, varför fynd av storsvuxna korsnäbbar inte nödvändigtvis behöver tillhöra arten *Loxia pytyopsittacus* som vi idag uppfattar den. Det äldsta kända korsnäbbfyndet är från äldre mellanpleistocen i Tjeckoslovakien. Tre fynd från den näst senaste istiden (130 000-200 000 år sedan) visar att korsnäbbar av både den mindre och den större korsnäbbens storlek då redan fanns i Västpalearktis.

Från den senaste istiden finns ca 30 fynd. De visar att korsnäbbar av den mindre korsnäbbens storlek fanns i Sydeuropa och Levanten under hela den senaste istiden samt att korsnäbbar av den större korsnäbbens storlek fanns åtminstone i ett begränsat område i västra Alperna mot istidens slut. Dessa sydeuropeiska korsnäbbar måste ha levat av tallfrö (eftersom inga andra barrträd förekom i området) och dessutom ha varit mer eller mindre helt isolerade från andra korsnäbbar i Sibirien. Ett fynd av en fossil undernäbb på Mallorca visar fö att korsnäbbarna där redan under den senaste istiden hade näbbar som var intermediära mellan mindre och större korsnäbb. Vid istidens slut spred sig korsnäbbarna norrut tillsammans med tallskogarna vilket framgår av fynd från Schweiz och England. Fossilfynden tillåter två alternativa hypoteser om de europeiska korsnäbbarnas härstamning beroende på om de storsvuxna korsnäbbarna i alpområdet tolkas som en separat art eller ej. Om de storsvuxna korsnäbbarna tillhörde *Loxia pytyopsittacus* så är denna en

relativt gammal art, och både mindre och större korsnäbb spred sig norrut tillsammans mot slutet av istiden. En av de båda arterna måste i så fall ha dött ut i Skottland och Sydeuropa och eventuella mindre korsnäbbar i Norden och på Europas fastland ha smält samman med från öster kommande "grankorsnäbbar".

Om de istida korsnäbbarna i medelhavsområdet tillhörde en enda variabel art blir bilden betydligt enklare. Både den

skotska korsnäbben, den nordiska större korsnäbben och de stornäbbade mediterrana raserna är i så fall troligen direkta avkomlingar av de istida "tallkorsnäbbarna" i Sydeuropa. Att den större korsnäbben avviker från de övriga beror då sannolikt på "character displacement" genom konkurrens med den mindre korsnäbben. Vilken av dessa båda teorier som är den rätta kan eventuellt avgöras genom DNA-undersökningar av de europeiska korsnäbbarna.