Direction of dispersion of cochineal *(Dactylopius coccus* Costa) within the Americas

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Dactylopius coccus has been used in Mexico and Peru as a source of natural dyes since pre-Columbian times. A phylogenetic analysis of the genus Dactylopius, and the disjoint distribution of D. coccus, suggest that the origin of D. coccus is South America and was introduced into North America by sea routes.

Key-words: cochineal, natural dyes, trading, Peru, Mexico

Introduction

Cochineal (*Dactylopius coccus* Costa; Hemiptera: Dactylopidae) is a sessile parasitic insect living on cladodes of prickly pear (*Opuntia ficus-indica* Miller; Cactaceae) and has been used as a source of natural dyes in Mesomerica and the Andean area since pre-Columbian times. The insects were used as tribute during the Aztec Empire and the Spanish domination of America. The dry insect was the second export product of the Mexican viceroyalty after silver. In an attempt to break the Spanish monopoly, the culture of the insects and their host plants expanded around the world under the guidance of the British government (Mann 1969). As a result of those early introductions which were not backed by thorough scientific knowledge, several species of *Opuntia* became serious weed problems in Australia and South Africa. They were successfully controlled only in the 1930s after the introduction of their natural enemies including some species of the genus *Dactylopius*. Due to their commercial value and their use as agents of biological control, some species of the insect genus have expanded their original distribution ranges and are presently found in places as distant as the Canary Islands, Australia, South Africa, Botswana, Nepal, India and Sri Lanka.

Phylogenetic analysis provide the opportunity to evaluate with independent evidences different historical hypotheses about the origin and distribution of animals and plants (Brown & Lomolino 1998). The family Dactylopiidae has only one genus, *Dactylopius*, with nine species, all of them originated in America and specialized in Cactaceae of the genus *Opuntia*. *D. tomentosus*, *D. confusus* and *D. opuntiae* inhabit North America (New Mexico, Arizona, Texas and Mexico), while *D. ceylonicus*, *D. austrinus*, *D. confertus* , *D. salmianus* and *D. zimmermanni* inhabit South America (Andean zones of northeast Argentina, Bolivia and Paraguay). The remaining species, *D. coccus*, has a disjoint distribution and is present in both hemispheres, in Mexico and Peru (FIGURE 1). The origin of *D. coccus* is controversial. The earliest evidence of use of the insect as a source

Some definitions of terms used in this article

Apomorphy: a derived character or character state.
Character: an observable feature of an organism.
Homoplasy: any character that is not a shared apomorphy.
Index of consistency: a measure of the amount of homoplasy in a data matrix corresponding to a given cladogram.
Ingroup: the group under investigations in the phylogenetic analysis.
Monophyletic group or Clade: a group which contains the most recent common ancestor and all descendant species.
Outgroup: a taxon (species or other category) used to make comparisons with the ingroup, in order to establish wheteher a state in the ingroup is primitive or derived.
Outgroup method: a method of indirect comparison that use the information in the outgroup in order to establish in the character under investigation the condition of plesiomorphism or apomorphism in the ingroup.
Phylogenetic tree: a graphic representation of genealogic relationships within a group.
Plesiomorphy: an ancestral or primitive character.

From Kitching *et al.* 1998.

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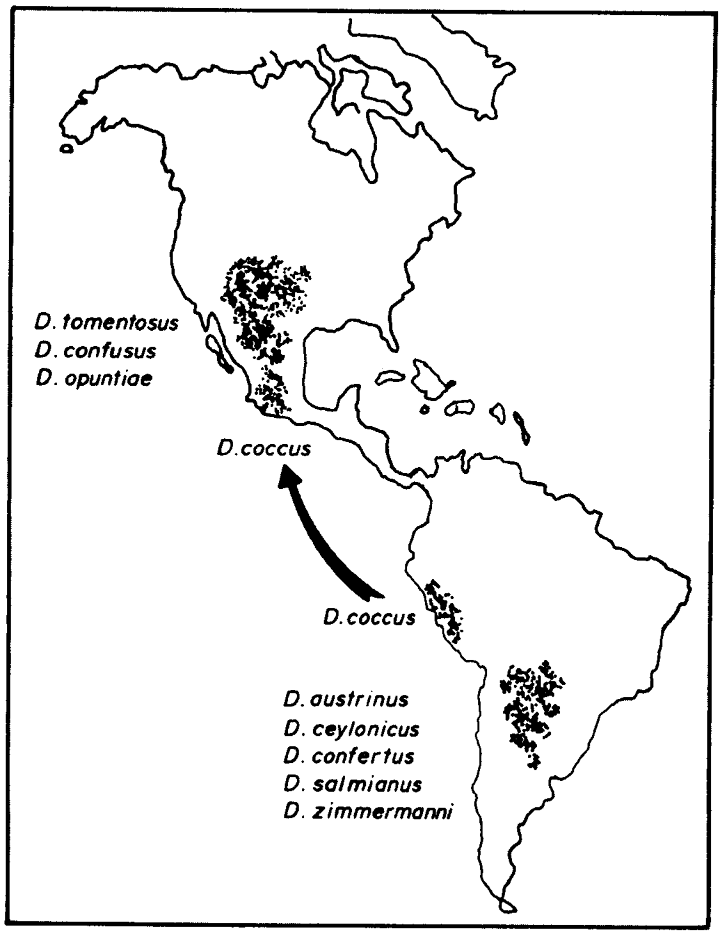

FIGURE 1. *Distribution of species of the genus* Dactylopius *in the Americas. The arrow indicates our proposal of south–north direction of dispersion of* Dactylopius coccus.

of dye was found in textiles from Paracas, Peru (Fester 1943; Yacovleff & Muelle 1934; Saltzman 1992), whereas evidence of cultivation and systematic exploitation of the insect were found in Tolteca settlements in Mexico (Pelham 1963; Brana 1964). Trading and coastal shipping between the Pacific Coast of the Andean area and Mesoamerica has occurred since 2200 BC and to southern Mexico since 1450 BC (Wolters 1999). Hence, it is likely that the presence of *D. coccus* both in Mexico and Peru is a consequence of introductions made with commercial purposes in pre-Columbian times. The aim of this study was to identify the hemisphere where the centre of origin of *D. coccus* is located, based on a phylogenetic reconstruction of the genus *Dactylopius*. The results of this first phylogenetic hypothesis could establish the direction (north–south or south–north) of the introduction of the insect and provide additional evidence of trading between pre-Columbian peoples.

Methods

A data matrix containing 51 morphological, ecological and chromosomal characters of adult females of the nine species of the genus (TABLES 1 & 2) was constructed making use of published information. Cladistic analysis was performed using the PAUP 3.1 program (Swofford 1993). The dataset was run using multiple parsimony and multistate characters were treated as unordered (changes of states 1–2 or 2–1 have the same probability to occur) and did not receive additional weight. Unknown characters were treated as lost. Characters were polarized as to the plesiomorphic (0 = primitive) or apomorphic (1, 2, etc = derived) states, based on the methodology of outgroup comparisons (Maddison *et al.* 1984). Briefly, the method consists in the selection of an external group, usually the sister group (the taxon genealogically closest to the ingroup), and the comparison of character states between the outgroup and the ingroup, in order to decide which characters are plesiomorphic or apomorphic. If a character state is present both in the outgroup and the ingroup, it is designated as plesiomorphic (by convention represented as '0'). Foldi (1997) suggested Kermesidae as sister group of Dactylopiidae, the anal ring being a shared character that characterizes the group. The polarization of the anal ring character suggests that bare anal ring is plesiomorphic in relation with anal ring with setae and pores. Due to the importance of this character and the obsolete anal ring (plesiomorphic) of *D. tomentosus* compared with its congeners (Pérez-Guerra & Kosztarab 1992), and because of lack of certainty in the relations between Dactylopiidae and the other families included in the Coccoidea, we opted in this work to use *D. tomentosus* as outgroup.

Results and discussion

The results of the cladistic analysis yielded only two cladograms both with tree length 124 and consistency index 0·589, differing only in the alternate position of *D. zimmermanni* and *D. confertus* as sister species of *D. coccus* (one tree is shown in FIGURE 2). The topology of the tree shows that the genus *Dactylopius* is monophyletic (they share a common ancestor) and that node 16 divides each tree into two branches which separate the genus biogeographically. Node 15 defines the South American *Dactylopius*, whereas node 13 defines the North American species. The result of cladistic analysis strongly suggests that *D. coccus* is a species of South American origin which has as sister spe-

(1) Pattern of wax: (0) cottony white; (1) powdery white.
(2) Tegument color: (0) purplish red; (1) brown.
(3) Number of head pores: (0) 2–4; (1) 5–6; (2) 7–11; (3) 12–15.
(4) Number of head clusters: (0) 20; (1) >20; (2) <20.
(5) Number of thorax pores: (0) 2–6; (1) 3–19; (2) 25–30.
(6) Number of thorax clusters: (0) 31–149; (1) 150–200; (2) 15–30.
(7) Number of abdominal pores: (0) <20; (1) >20.
(8) Number of abdominal clusters: (0) 100–200; (1) >200; (2) <100.
(9) Presence of ducts: (0) no; (1) yes.
(10) Number of ducts: (0) 2–4; (1) 7–8.
(11) Number of setae: (0) few; (1) many.
(12) Distribution of setae: (0) abdominal; (1) all over the body
(13) Kind of setae: (0) various forms (1) cylinder-shaped; (2) slim; (3) truncated cylinder-shaped.
(14) Antennal segments: (0) 7; (1) 6.
(15) Number of setae in antennae: (0) 11; (1) 12; (2) 14; (3) 16.
(16) Number of fleshy setae in antennae: (0) 6; (1) <6.
(17) Number of setae in the first antennal segment: (0) 3; (1) 4.
(18) Number of setae in the third antennal segment: (0) 0; (1) 2.
(19) Number of setae in the fourth antennal segment: (0) 2; (1) 0; (2) 4.
(20) Number of setae in the fifth antennal segment: (0) 1; (1) >1.
(21) Setae number in the sixth antennal segment: (0) 1; (1) 2; (2) 4.
(22) Setae number in the seventh antennal segment: (0) <4; (1) >4.
(23) Number of fleshy setae in the fourth antennal segment: (0) 0; (1) 1.
(24) Number of fleshy setae in the fifth antennal segment: (0) 0; (1) 1.
(25) Number of fleshy setae in the sixth antennal segment: (0) 3; (1) 1.
(26) Number of fleshy setae in the seventh antennae segment: (0)>1; (1) 0.
(27) Process associated to spiracle: (0) present; (1) absent.
(28) Number of pores associated to spiracles: (0) 1; (1) 2.
(29) Shape of anal ring: (0) circular; (1) ellipsoidal.
(30) Number of anal clusters: (0) 1; (1) >1.
(31) Width of anal zone (mm): (0) 200–300; (1) >300; (2) <200
(32) Length of anal zone (mm) (0) <100; (1) >100
(33) Claw denticles: (0) absent; (1) present
(34) Comparative size of segments: (0) Meta>Meso>Proto; (1) Meta>Proto>Meso; (2) Proto>Meta>Meso.
(35) Length of extremities (mm): (0) 300–399; (1) 400–599; (2) 600–900.
(36) Abdominal setae: (0) lateral; (1) all over the surface.
(37) Tubular ducts: (0) in head and thorax; (1) in head, thorax and abdomen (2) in abdomen.
(38) Vulvar area pores: (0) present; (1) absent.
(39) Vulvar area setae: (0) present; (1) absent.
(40) Vulvar area ducts: (0) present; (1) absent.
(41) Host range: (0) 1 series; (1) 2–5 series; (2) 6 series; (3) 11 series.
(42) Subgenus Cilindropuntia:(0) host ; (1) non-host.
(43) Subgenus Platyopuntias: (0) non-host; (1) host.
(44) Series ficus indicae: (0) non-host; (1) host.
(45) Series dillenianae: (0) non-host; (1) host.
(46) Series streptacanthae:(0) non-host ; (1) host.
(47) Series elatae: (0) non-host; (1) host.
(48) Biomes: (0) desert; (1) mountain.
(49) Natural enemies: (0) none described; (1) described.
(50) Dye: (0) < 12% carminic acid; (1) >12% carminic acid.
(51) Chromosomes: (0) 4 short pairs and 1 long pair; (1) 8 short pairs.

TABLE 1. *Definition and state of characters for the genus* Dactylopius.

	012345678901234567890123456789012345678901
	123456789111111111122222222223333333333444444444455
austrinus	010001101000111101102?11010011110020001001100001l0?
ceylonicus	110200001010311101102?1101001?200200101111111101110?
coccus	103120120100203110200100101111010121210011110l0?111
confertus	??221011110110311001110110001020111020000100000100?
confusus	001100110110102110011101100010200010100020111010100
opuntiae	000000110011101010010001100010200000100130100000000
salmianus	0?0202020000102010001001100010200000100000000000110?
tomentosus	000000000000000000000001100000??000000001000000000100
zimmermann	??100011000010311000010110101101001010000100000110?

unknown values = ?

TABLE 2. *Character matrix used in the cladistic analysis of genus* Dactylopius.

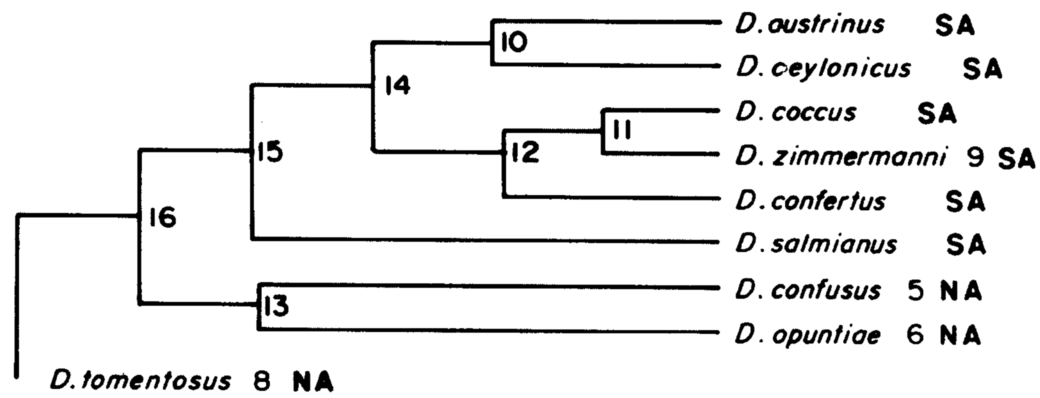

FIGURE 2. *Phylogenetic tree of the genus* Dactylopius, *arising from the cladistic analysis of data shown in* TABLE 1. SA *indicates species of South American origin,* NA *indicates species of North American origin. Node 15 defines the South American* Dactylopius, *where* D. coccus *is included.*

cies *D. zimmermanni* or *D. confertus*, both of South American origin as well. The position of *D. coccus* in the phylogeny, the limited dispersion capability of the mobile stages of the insect, and the restricted natural distribution of the species, suggest that the presence of *D. coccus* in Mesoamerica is a consequence of human action and that introduction was realised in the south–north direction. The presence of cochineal in Mexico and Peru at the arrival of the Spanish conquerors indicates that this introduction was made in pre-Columbian times. There is evidence of Transamerican dispersion of useful neotropical vegetables in pre-Columbian times (Brucher 1988; 1990), crop plant exports having occurred both from the Andes to Mesoamerica and Mexico (sweet manioc, custard apple, early great-grained corn) and in the inverse way, from Mexico to the Andean area (avocado, chile peppers). Based on the distribution of sweet manioc and cacao, Wolters (1999) suggests that a Pacific sea route was used for the introduction of both products, since neither wild cacao trees nor primitive cultigens were found in the area between Ecuador and Guatemala. Similarly, the Pacific trading sea route could explain the disjoint distribution of *D. coccus* because that species is not found anywhere between Peru and Southern Mexico, and a land transporting route would have spread that valuable product along America. Within the management techniques developed by the ancient peoples of the Americas, infested cladodes were moved from one place to another to protect the insect colonies from adverse environmental conditions (i.e. wind, rain) and also to assure enough insects to re-infest the field (Baranyovitz 1979). The same technique could have been used for the sea transport and introduction of the insect from South America to Mesoamerica. In conclusion, phylogenetic analysis of the genus *Dactylopius* suggests that the cochineal *D. coccus* originated in South America and its disjoint distribution suggests that it was most likely transported to North America by sea.

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D-Day sites in England: an assessment

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Between midnight on 6 June (D-Day) and 30 June 1944, over 850,000 men landed on the invasion beachheads of Normandy, together with nearly 150,000 vehicles and 570,000 tons of supplies. Assembled in camps and transit areas over the preceding months, this force was dispatched from a string of sites along Britain's coastline between East Anglia and South Wales (Dobinson 1996: 2). The article reviews those sites in England involved in this embarkation. English Heritage's Monuments Protection Programme (MPP) aims to identify surviving sites and recommend appropriate protection for them.

Key-words: D-Day archaeology, Monument Protection Programme, Normandy, differential preservation, heritage

This paper describes those monuments surviving in England which represent the preparations and embarkation for the Normandy invasions of 1944 (see Dobinson *et al.* 1997 for a summary of the wider project of which this study forms a part). Contrary to what has been said previously (e.g. Wills 1994), much of this archaeological record does survive including examples of all types of site constructed or adapted to serve Operation *Neptune* — the assault phase of *Overlord* — which represented the springboard for the Allied invasion of Ger-

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