

Paléoenvironnements en Europe et région méditerranéenne au Cénozoïque



Bassin de Boudinar, Maroc

Notice de candidature pour l'obtention de l'HDR
Université de Montpellier
Ecole doctorale GAIA

Séverine FAUQUETTE
CR CNRS, ISEM

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Curriculum Vitae

Séverine FAUQUETTE

46 ans, 3 enfants

Chargée de Recherche CNRS 1^{ère} classe

Adresse professionnelle

Institut de Sciences de l'Evolution, Université de Montpellier, CNRS, IRD, EPHE

Département Paléoenvironnements

Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier cedex 5

Tél : 04 67 14 41 79

e-mail : severine.fauquette@umontpellier.fr

Page web: http://www.isem.univ-montp2.fr/fauquette_severine

Titres

Doctorat en Sciences, spécialité Biologie des Populations et Ecologie, Université d'Aix-Marseille 3, **1998**. « Le climat du Pliocène : nouvelle méthode de quantification basée sur les données polliniques et application à la Méditerranée occidentale ». Sous la direction de Joël Guiot et Jean-Pierre Suc. Mention très honorable avec les félicitations du jury.

DEA Ecosystèmes Continentaux Arides, Montagnards et Méditerranéens, Université Aix-Marseille 3, **1993**. « Histoire de la végétation forestière et fluctuations de la timberline dans un site du briançonnais (Hautes-Alpes, France) : étude paléoécologique (pollen et macrorestes) du lac de Cristol ». Sous la direction de Maurice Reille et Jacques-Louis de Beaulieu.

Maîtrise de Sciences Naturelles, Université de Mont Saint Aignan, Rouen, **1992**

Licence de Sciences Naturelles, Université de Mont Saint Aignan, Rouen, **1991**

DEUG Sciences de la Nature et de la Vie, Université de Mont Saint Aignan, Rouen, **1990**

Baccalauréat série D, **1988**

Parcours professionnel

- 1995-1997 **CDD** sur projets ANDRA (voir la liste des projets de recherche)
- 1997-1999 Postes d'**ATER** Université d'Aix-Marseille 3
- Début 2000 **Post-doctorat** à l'Université de Tübingen, Allemagne (6 mois)
- 2000-2003 **Chargée de recherche 2^{ème} classe** au CNRS, recrutée au labo Paléobiosphère et Paléoenvironnements à Lyon 1
- Début 2004 Mutation (sur ma demande) à l'ISEM, Montpellier
- 2005- **Chargée de recherche 1^{ère} classe** au CNRS à l'ISEM, Montpellier

Mon parcours professionnel a été entrecoupé de **3 congés de maternité** : du 1.09.2000 au 1.01.2001 ; du 24.04.2004 au 14.09.2004 ; du 21.04.2007 au 19.10.2007.

Qualifications

Qualification aux fonctions de Maître de Conférence, **sections 36 et 67**, en 1999.

Prix et bourses

- Prix de l'**Association des Palynologues de Langue Française** (remis le 14. 09. 1999)
- Prix de la **Fondation Emberger** (remis le 2. 12. 1999)
- Bourse « jeune chercheur » du **Comité National Français de Géologie** (1999)
- Bourse « jeune chercheur » du **Comité d'organisation XVI^{ème} International Botanical Congress** (Saint Louis, Missouri, Etats-Unis, 1999).
- Bourse post-doctorale **Alexander von Humboldt** (2000)

Responsabilités scientifiques et administratives

2001 – 2013 Trésorière de l'Association des Palynologues de Langue Française (l'APLF)

2010 – 2016 Membre du pool d'experts de l'Université de Montpellier, section 36

2015 – Membre élu du Conseil de Laboratoire (ISEM)

2015 – Co-responsable de la collection de référence palynologique et du plateau microscopie pour la palynologie

Activité éditoriale

2001 – 2003 Membre du Comité d'édition de la revue *Geobios*

2004 – 2013 Membre du Comité Scientifique de la revue *Geobios*

2014 – Editeur Associé de la revue *Geobios*

Activité d'évaluation

Evaluation de manuscrits pour les revues :

Global Biogeography and Ecology – Palaeogeography, Palaeoclimatology, Palaeoecology – Quaternary International – *Geobios* – *Geodiversitas* – *Bolletino della Societa paleontologica Italiana* – *Review of Palaeobotany and Palynology* – *Earth and Planetary Science Letters*

Evaluation de projets de recherche

Programme PALEO2 de l'INSU

Austrian Science Foundation (FWF)

The Netherland Organisation for Scientific Research (NWO)

Jury de thèse

Gonzalo Jiménez-Moreno (2005), Université de Grenade, Co-encadrante.

Enseignement

J'ai pris part à des tâches d'enseignement très rapidement puisque j'ai commencé pendant ma Licence à l'Université de Rouen : j'ai été, pendant 2 ans, assistante de travaux pratiques pour seconder les enseignants en charge des TP. C'est également, à mon avis, une façon d'encadrer des étudiants et de les mener vers la recherche.

- ✓ 1991 – 1992 Assistante Travaux Pratiques en DEUG, *TP de biologie végétale*, **Université de Rouen**, 30 heures annuelles
- ✓ 1991 – 1992 Assistante Travaux Pratiques en DEUG, *TP de géologie*, **Université de Rouen**, 30 heures annuelles
- ✓ 1995 – 1997 Vacataire, *TP de biologie végétale*, **Université d'Aix-Marseille 3**, 30 heures annuelles
- ✓ 1995 – 1997 Vacataire, *TD de génétique*, **Université d'Aix-Marseille 3**, 20 heures annuelles
- ✓ 1997 – 1999 **ATER**, CM et TP de *biologie végétale* (anatomie végétale, cycles de vie), CM et TD d'*écologie*, TD de *statistiques*, **Université d'Aix-Marseille 3**, 192 h annuelles
- ✓ 2005 – 2011 CM *Histoire et évolution des végétaux et environnements* (HIVEN), **Université de Montpellier 2**, 2 heures annuelles
- ✓ 2006 – 2007 TD de *biologie végétale*, **Université de Montpellier 2**, 12 heures annuelles
- ✓ 2006 – 2011 CM *Paléoclimatologie du Néogène* en Master 2, **Université de Montpellier 2**, 2 heures annuelles
- ✓ 2011 – TP en L2, *Diversité et évolution des végétaux actuels et fossiles*. **Université de Montpellier 2**, 36 heures annuelles.
- ✓ 2016 – TD en Master 1 CEPAGE : *La crise de salinité Messinienne : la controverse*. **Université de Montpellier**, 3h.

Encadrement d'étudiants

LICENCE

2007 Monica Piccinno, étudiante Erasmus, Licence **Archéologie**, Université Paul Valéry - Montpellier 3.

MASTER 1

2001 Scander Safsaf, Maîtrise **Sciences de la Terre et de l'Univers**, Université Claude Bernard, Lyon 1, co-encadrement (50%) avec J.-P. Suc.

2015 Augustin Feussom, Master 1 **BVT**, Ecole Doctorale SIBAGHE, Université de Montpellier, co-encadrement (80%) avec M.-P. Ledru.

MASTER 2

2002 Véronique Charlet, DEA **Paléontologie et Environnements sédimentaires**, Ecole Doctorale Evolution Ecosystèmes Microbiologie Modélisation (E2M2), Univ. Lyon 1, co-encadrement (40%) avec J.-P. Suc et R. Cheddadi.

2003 Sébastien Joannin, DEA **Paléontologie et Environnements sédimentaires**, Ecole Doctorale E2M2, Université Lyon1, co-encadrement (20%) avec J.-P. Suc, F. Quillevéré et E. Cortijo.

2012 Mohamed Imsalem, Master 2 **PPP**, Ecole Doctorale SIBAGHE, Université Montpellier 2, co-encadrement (60%) avec S. Muller.

2016 Augustin Feussom, Master 2 **BIOGET**, Ecole Doctorale GAIA, Université de Montpellier, co-encadrement (80%) avec M.-P. Ledru.

DOCTORAT

2002-2005 Gonzalo Jiménez-Moreno, **Thèse de Doctorat**, cotutelle Université Lyon1 et Université de Grenade (Espagne), co-encadrement (30%) avec J.-P. Suc et P. Rivas-Carrera.

Participation ponctuelle à des encadrements sans cadre officiel

2009-2011 Marianna Ricci, **Thèse de Doctorat** à l'Université de Florence, Italie, co-encadrement (5%) avec Adele Bertini.

2012-2016 Mohammed Achalhi, **Thèse de Doctorat** en co-tutelle Université de Montpellier, et Université de Oujda (Maroc), co-encadrement (5%) avec P. Münch, G. Merzeraud et A. Azdimoussa.

Projets de recherche

- 1995 – 1998 Projets financés par l'ANDRA:
1 - *Reconstitution de la végétation depuis l'interglaciaire eémien et enchaînements possibles – cas de la région de la Vienne* ; **2** - *Estimation de la durée de vie des écosystèmes climaciques* ; **3** - *Estimation des valeurs des paramètres abiotiques pour les trois biomes majeurs ayant existé en France au cours du dernier cycle glaciaire-interglaciaire*. Responsable : J. Guiot.
- 1999 – 2004 **GdR Marges** (CNRS, IFREMER, TOTAL-ELF-FINA): Atelier Golfe du Lion. Coordinateur : S. Berné (IFREMER).
- 2000 – 2004 **European Science Foundation**: "Environments and Ecosystem Dynamics of the Eurasian Neogene (EEDEN)". Coordinateur : J. Meulenkamp (Utrecht).
- 2000 – 2002 **Institut Français de la Biodiversité**: "La diversité végétale du domaine méditerranéen : son évolution depuis 6 Ma". Responsables : **S. Fauquette** et J.-P. Suc.
- 2001 – 2004 **Programme ECLIPSE** du CNRS: "La crise de salinité messinienne : modalités, conséquences régionales et globales, quantifications". Coordinateurs : J.-M. Rouchy et J.-P. Suc.
- 2003 – 2004 **Programme ECLIPSE** du CNRS: "Quantification de l'impact des forçages climatiques/anthropiques passés et futurs sur les circulations dans le Bassin de Paris". Responsable : S. Violette (UMR 7619-*Sisyphé*, Laboratoire de Géologie Appliquée, Paris). Co-financé par l'ANDRA, EDF, GDF, IRSN.
- 2003 – 2005 **Institut Français de la Biodiversité**: "Un atelier exceptionnel d'étude de la dynamique de la biodiversité végétale : la Camargue d'il y a 6000 ans à demain". Responsable: J.-P. Suc (Univ. Lyon 1).
- 2005 – 2006 **Programme ECLIPSE** du CNRS : "Environnements quaternaires du Petit Caucase: forçage du volcanisme, des glaciations et de l'Homme". Responsables: C. Chataigner (Archéorient, Univ. Lyon 2), P. Roiron (CBAE, Univ. Montpellier).
- 2009 – 2012 **ANR Programme blanc**, Sciences de l'Univers et Géo-environnement : "ERD-Alps: Erosion and Relief Development in the Western Alps". Responsable: P. Van Der Beek (LGCA, Univ. Joseph Fourier, Grenoble).
- 2011 – 2012 **Ministère Italien de l'Enseignement Supérieur et de la Recherche**: "Palaeobiological signals of climatic gradients and hydrologic changes during the Messinian Salinity Crisis". Responsables: M. Roveri et A. Bertini (Université de Florence, Italie).
- 2011 – 2012 **Programme MISTRALS, PaleoMEx** : "CYCLAMEN - CYCLicity and interglaciAl periods in the MEditerranean". Responsable: N. Combourieu-Nebout (LSCE, Gif sur Yvette)
- 2011 – 2015 **PHC Egide Volubilis** : « Morphogénèse récente (Néogène à actuelle) de la marge marocaine de la Méditerranée (Rif) : Tectonique vs érosion. Responsable : Ph. Münch (Geosciences Montpellier).

- 2012 – 2016 **ANR programme blanc**, Sciences de l'Univers et Géo-environnement : « PYRAMID ». Responsable : M. Ford (CRPG Nancy).
- 2014 – 2018 **IRSES, Programme Personnes du 7^{ème} PCRD**. Projet MEDYNA – Maghreb-Europe research staff exchange on GeoDynamics, Geohazards, and applied geology in North West Africa. Responsables : C. Garrido (Univ. Grenade, Espagne), J.-L. Bodinier (Geosciences Montpellier).
- 2016 – 2017 **Labex CEBA** (Toulouse/Cayenne/Montpellier). Projet « **Source**: *Seeking the sources of terrestrial biodiversity in French Guiana by enhancing the fossil record* ». Responsable : P.O. Antoine (ISEM)

Collaborations

Mes principales collaborations sont avec des chercheurs de laboratoires nationaux ou internationaux parmi lesquels :

Géosciences Montpellier

Histoire naturelle de l'homme préhistorique, MNHN, Paris

Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale, Marseille

Institut des Sciences de la Terre (ISTERRE), Grenoble

Institut des Sciences de la Terre de Paris (ISTEP)

Laboratoire de Géologie de Lyon – Terre, Planètes, Environnement (LGLPTE)

Département des Sciences de la Terre, Univ. Florence, Italie

Département de Stratigraphie et Paléontologie, Univ. Grenade, Espagne

Département des Sciences de la Terre, Univ. Canton, Chine

Laboratoire des Géosciences Appliquées, Univ. Oujda, Maroc

Département de Géologie, Univ. Tétouan, Maroc

Laboratoire Biodiversité et dynamique des écosystèmes, Univ. Marrakech, Maroc

Liste exhaustive des publications

h-index : 16

49 productions dont :

- 33 publications de rang A (11 en premier auteur)
- 3 chapitres de livre (2 en premier auteur)
- 9 publications dans des revues à comité de lecture non indexées ou actes de colloques
- 4 rapports d'étude dont 3 pour l'ANDRA

Le tableau suivant donne la répartition de mes articles dans les revues de rang A avec leur IF.

<i>Revue</i>	Nombre d'articles	IF (2015)
<i>Earth and Planetary Science Letters</i>	5	4.326
<i>Journal of Biogeography</i>	1	3.997
<i>Climate of the Past</i>	1	3.638
<i>Global and Planetary Change</i>	1	3.548
<i>Palaeogeogr., Palaeoclimatol., Palaeoecol.</i>	9	2.525
<i>Boreas</i>	1	2.386
<i>Review of Palaeobotany and Palynology</i>	5	2.158
<i>Quaternary International</i>	1	2.067
<i>Vegetation History and Archaeobotany</i>	1	2.039
<i>Journal of Arid Environments</i>	1	1.623
<i>Comptes-Rendus de l'Acad. des Sci., Geosciences</i>	1	1.610
<i>Geobios</i>	2	1.151
<i>Comptes-Rendus de l'Acad. des Sci., Biologies</i>	1	1.064
<i>Bulletin de la Société Géologique de France</i>	1	0.955
<i>Ecoscience</i>	1	0.595
<i>Comptes-Rendus de l'Acad. des Sci., Série II</i>	1	0.731 (1997)

Liste exhaustive de mes productions :

PUBLICATIONS SOUMISES

1. Suan G., Popescu S., Suc J.-P., Schnyder J., **Fauquette S.**, Baudin F., Yoon D., Piepjohn K., Sobolev P., Labrousse L., soumis. Evidence for subtropical warmth in Arctic Eurasia during the Early Eocene. *Geology*.

PUBLICATIONS DE RANG A (les étudiants que j'ai co-encadrés sont soulignés)

33. Achalhi M., Münch P., Cornée J.-J., Azdimousa A., Melinte-Dobrinescu M., Quillévéré F., Drinia H., **Fauquette S.**, Jimenez-Moreno G., Merzeraud G., Ben Moussa A., El Kharim Y., Feddi N., 2016. The late Miocene Mediterranean-Atlantic connections through the North Rifian Corridor: new insights from the Boudinar and Arbaa Taourirt basins (northeastern Rif, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 459, 131-152.

32. **Fauquette S.**, Bertini A., Manzi V., Roveri M., Argnani A., Menichetti E., 2015. Reconstruction of the Northern and Central Apennines (Italy) palaeoaltitude during the late Neogene from pollen data. *Review of Palaeobotany and Palynology*, 218, 117-126.
31. Combourieu-Nebout N., Bertini A., Russo Ermolli E., Peyron O., Klotz S., Montade V., **Fauquette S.**, Allen J., Fusco F., Goring S., Huntley B., Joannin S., Lebreton V., Magri D., Martinetto E., Orain R., Sadori L., 2015. Climate Changes in central Mediterranean and Italian vegetation dynamics since the Pliocene. *Review of Palaeobotany and Palynology*, 218, 127-147.
30. Ricci M., Bertini A., Capezzuoli E., Horvatincic N., Andrews J.E., **Fauquette S.**, Fedi M., 2015. Palynological investigation of a Late Quaternary calcareous tufa and travertine deposit: the case study of Bagnoli in Valdelsa Basin (Tuscany, central Italy). *Review of Palaeobotany and Palynology*, 218, 184-197.
29. **Fauquette S.**, Bernet M., Suc J.-P., Grosjean A.-S., Guillot S., van der Beek P., Jourdan S., Popescu S.M., Jiménez-Moreno G., Bertini A., Pittet B., Tricart P., Dumont T., Schwartz S., Zheng Z., Roche E., Pavia G., Gardien V., 2015. Quantifying the Eocene to Pleistocene topographic evolution of the southwestern Alps, France and Italy. *Earth and Planetary Science Letters*, 412, 220-234.
28. Muller S.D., Rhazi L., Andrieux B., Bottollier-Curtet M., **Fauquette S.**, Saber E.-R., Rifai N., Daoud-Bouattour A., 2014. Late-Holocene vegetation dynamics and human disturbance in West Rif Mountains (NW. Morocco). *Vegetation History and Archaeobotany*, DOI 10.1007/s00334-014-0504-9.
27. Cornée J.-J., Münch P., Melinte-Dobrinescu M., Ben Moussa A., Quillévéré F., Drinia H., Azdimoussa A., Merzeraud G., **Fauquette S.**, Corsini M., Feddi N., 2014. The Pliocene reflooding in the Western Mediterranean: new insights from the rias of the Internal Rif, Morocco. *Comptes Rendus Geosciences*, 346, 90-98.
26. Amami B., Rhazi L., Chaibi M., **Fauquette S.**, Ayt Ougougdal M., Charif A., Ridaoui M., Bouahim S., Carré M., Daoud-Bouattour A., Grillas P., Muller S.D., 2013. Late Quaternary history of a Mediterranean temporary pool from western Morocco based on sedimentological and palynological evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 392, 281-292.
25. **Fauquette S.**, Combourieu-Nebout N., 2013. Palaeoaltitude of the Sila Mountain (Southern Apennines, Italy) and distribution of the vegetation belts at ca. 2.4 Ma (Early Pleistocene). *Review of Palaeobotany and Palynology*, 189, 1-7.
24. Suc J.-P., **Fauquette S.**, 2012. The use of pollen floras as a tool to estimate palaeoaltitude of mountains: the Eastern Pyrenees in the Late Neogene, a case study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 321-322, 41-54.
23. Feddi N., **Fauquette S.**, Suc J.-P., 2011. Histoire plio-pléistocène des écosystèmes végétaux de Méditerranée sud-occidentale: apport de l'analyse pollinique de deux sondages en Mer d'Alboran. *Geobios*, 44, 57-69.
22. Bertini A., Magi M., Mazza P., **Fauquette S.**, 2010. Impact of short-term climatic events on latest Pliocene land settings and communities in Central Italy (Upper Valdarno basin). *Quaternary International*, 225, 92-105.

21. Jiménez-Moreno G., **Fauquette S.**, Suc J.-P., 2010. Miocene to Pliocene vegetation and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaeobotany and Palynology*, 162, 403-415.
20. Carrión J.S., Fernández S., Jiménez-Moreno G., **Fauquette S.**, González-Sampériz P., Finlayson C., 2010. The historical origins of aridity and vegetation degradation in southeastern Spain. *Journal of Arid Environments*, 74, 731-736.
19. Jost A., **Fauquette S.**, Kageyama M., Krinner G., Ramstein G., Suc J.-P., Violette S., 2009. High resolution climate and vegetation simulations of the Mid-Pliocene, a model-data comparison over western Europe and the Mediterranean region. *Climate of the Past*, 5, 585-606.
18. Melinte-Dobrinescu M. C, Suc J.-P., Clauzon G., Popescu S.M., Meyer B., Armijo R., Biltekin D., Çağatay N., Uçarkus G., Jouannic G., **Fauquette S.**, Çakir Z., 2009. The Messinian Salinity Crisis in the Dardanelles region: chronostratigraphic constraints. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 278, 24-39.
17. Jiménez-Moreno G., **Fauquette S.**, Suc J.-P., 2008. Vegetation, climate and paleoaltitude reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria, Central Europe. *Journal of Biogeography*, 35, 1638-1649.
16. Jiménez-Moreno G., **Fauquette S.**, Suc J.-P., Abdul Aziz H., 2007. Early Miocene repetitive vegetation and climatic changes in the lacustrine deposits of the Rubielos de Mora basin (Teruel, NE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 250, 101-113.
15. Muller S.D., Nakagawa T., de Beaulieu J.-L., Court-Picon M., **Fauquette S.**, Genries A., 2006. Paléostrutures de végétation à la limite supérieure des forêts dans les Alpes françaises internes. *Comptes-rendus Biologie*, 329, 502-511.
14. **Fauquette S.**, Suc J.-P., Bertini A., Popescu S. M., Warny S., Bachiri Taoufiq N., Perez Villa M. J., Chikhi H., Feddi N., Subally D., Clauzon G., Ferrier J., 2006. How much did the climate force the Messinian salinity crisis? Quantified climatic conditions from pollen records in the Mediterranean region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238, 281-301.
13. Klotz S., **Fauquette S.**, Combourieu Nebout N., Uhl D., Suc J.-P., Mosbrugger V., 2006. Seasonality intensification and long-term winter cooling as a part of the late Pliocene climate development. *Earth and Planetary Science Letters*, 241, 174-187.
12. Jiménez-Moreno G., Rodríguez-Tovar F.J., Pardo-Igúzquiza E., **Fauquette S.**, Suc J.-P., Muller P., 2005. High-resolution palynological analysis in late Early-Middle Miocene Tengellic-2 core from the Pannonian Basin, Hungary: Climatic changes, astronomical forcing and eustatic fluctuations in the Central Paratethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 216, 73-97.
11. **Fauquette S.**, Bertini A., 2003. Quantification of the northern Italy Pliocene climate from pollen data – evidence for a very peculiar climate pattern. *Boreas*, 32 (2), 361-369.
10. Roger S, Coulon C., Thouveny N., Féraud G., Van velzen A., **Fauquette S.**, Cochemé J.-J., Prévot M., Verosub K.L., 2001. Reply to the comment on « $^{40}\text{Ar}/^{39}\text{Ar}$ dating of a tephra layer in the Pliocene Senèze maar lacustrine sequence (French Massif Central): constraint on the age of the Réunion-Matuyama transition and implications on paleoenvironmental archives ». *Earth and Planetary Science Letters*, 192, 629-630.

9. Roger S, Coulon C., Thouveny N., Féraud G., Van velzen A., **Fauquette S.**, Cochemé J.-J., Prévot M., Verosub K.L., 2000. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of a tephra layer in the Pliocene Senèze maar lacustrine sequence (French Massif Central): constraint on the age of the Réunion-Matuyama transition and implications on paleoenvironmental archives. *Earth and Planetary Science Letters*, 183 (3-4), 431-440.
8. Torre F., Guiot J., **Fauquette S.** et Menut-Calvez M., 2000. Reconstruction of the abiotic characteristics of past biomes: an example from the last glacial-interglacial cycle in France. *Ecoscience*, 7 (4), 491-500.
7. Combourieu-Nebout N., **Fauquette S.** et Quézel P., 2000. What was the Late Pliocene Mediterranean climate like: a preliminary quantification from vegetation. *Bulletin de la Société Géologique de France*, 171 (2), p. 271-277.
6. **Fauquette S.**, Guiot J., Menut M., Beaulieu J.-L. de, Reille M. et Guenet P., 1999. Vegetation and climate since the Last Interglacial in the Vienne area (France). *Global and Planetary Change*, 20, 1-17.
5. **Fauquette S.**, Clauzon G., Suc J.-P. et Zheng Z., 1999. A new approach for paleoaltitude estimates based on pollen records: example of the Mercantour Massif (Southeastern France) at the Earliest Pliocene. *Earth and Planetary Science Letters*, 170, 35-47.
4. **Fauquette S.**, Suc J.-P., Guiot J., Diniz F., Feddi N., Zheng Z., Bessais E. et Drivaliari A., 1999. Climate and biomes in the West Mediterranean area during the Pliocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 152, 15-36.
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Synthèse des travaux scientifiques

Préambule

Mes premiers travaux de recherche réalisés dans le cadre de mon DEA à l'IMEP (l'actuel *IMBE*, Univ. Aix-Marseille) portaient sur l'étude palynologique du lac de Cristol (Hautes-Alpes, France). Ils m'ont permis de retracer l'histoire de la végétation forestière et les fluctuations de la limite supérieure des forêts dans cette région depuis le Tardiglaciaire (Fauquette, 1995 ; Fauquette et Talon, 1995).

Rapidement, j'ai éprouvé le besoin d'aller plus loin avec les données polliniques, ne pas s'arrêter à la reconstitution de la végétation, mais également de les utiliser comme outil pour d'autres reconstitutions, en particulier quantitatives, parce que la palynologie se situe à l'interface de plusieurs champs disciplinaires : les sciences de la vie (biologie, écologie, biogéographie), les sciences de la Terre (géologie, géomorphologie, climatologie, sédimentologie) et les sciences de l'homme (archéologie, ethnobotanique).

A la fin de mon DEA, j'ai rencontré Jean-Pierre Suc, palynologue, spécialiste du Néogène rattaché à l'ISEM à cette époque, qui souhaitait valoriser ses nombreuses données polliniques en reconstituant le climat de façon quantifiée, à l'instar des palynologues travaillant sur les périodes plus récentes (les 2 derniers cycles climatiques).

C'est donc encadrée par Jean-Pierre Suc et Joël Guiot, spécialiste en paléoclimatologie (à l'IMEP à l'époque, au CEREGE actuellement), que j'ai préparé ma thèse à l'IMEP. Elle s'intitulait « Le climat du Pliocène : nouvelle méthode de quantification basée sur les données polliniques et application à la Méditerranée occidentale ». Cette thèse m'avait également permis de rencontrer et de travailler avec le professeur Pierre Quézel, éminent botaniste de Marseille, spécialiste de la flore et la végétation méditerranéenne.

Je ne suis donc pas (plus) palynologue à proprement parlé car je ne pratique plus l'analyse pollinique. Mes travaux m'ont alors amenée à collaborer avec des palynologues spécialistes du Néogène, en particulier Jean-Pierre Suc (DR CNRS émérite, ISTEP, Paris 6), Adèle Bertini (Départ. des Sciences de la Terre, Univ. Florence, Italie), Gonzalo Jiménez-Moreno (Départ. de stratigraphie et paléontologie, Univ. Grenade, Espagne), Nathalie Combourieu-Nebout (Histoire naturelle de l'homme préhistorique, MNHN), Zhuo Zheng (Départ. des Sciences de la Terre, Univ. Canton, Chine), Filomena Diniz (Départ. de Géologie, Univ. Lisbonne), Mustapha Bessedik (Sciences de la Terre, Univ. Oran, Algérie). Ils sont tous co-auteurs des publications dans lesquelles sont utilisées leurs données.

Depuis le début de ma thèse, mes travaux m'ont permis d'avoir des collaborations avec des palynologues, des botanistes, des géologues et des modélisateurs du climat avec lesquels j'ai pu avoir des discussions indispensables et fructueuses qui donnent à mes travaux une grande valeur ajoutée et une portée qu'ils n'auraient pas eue sans ces collaborations.

J'en profite ici pour remercier tous ceux qui m'ont aidée et soutenue depuis mon DEA. Merci à mes collègues et amis marseillais, lyonnais et montpelliérains (et ceux qui sont les deux voire les trois à la fois !). Un merci tout particulier à Laurent Bremond qui m'a un peu bousculée pour que je prépare mon HDR et à Jean-Jacques Cornée qui a relu le manuscrit. Merci à ma famille, à Michel et mes titous, Justin, Colline et Clémentine, à qui je dédie ce tout petit morceau d'histoire de notre Terre.

La synthèse que je présente ici ne se veut pas exhaustive, je n'y ai pas intégré tous mes travaux afin de ne pas perdre le fil conducteur de mes recherches et de faire en sorte que ce document reste agréable à lire.

Paléoenvironnements en Europe et région méditerranéenne au Cénozoïque

Introduction

Le Cénozoïque (66 millions d'années – Actuel) est une période qui voit des modifications climatiques très intenses, faisant passer la Terre du *greenhouse climate* du début du Cénozoïque au *icehouse climate* de la fin du Cénozoïque (Fig. 1 ; Zachos et al., 2001, 2008).

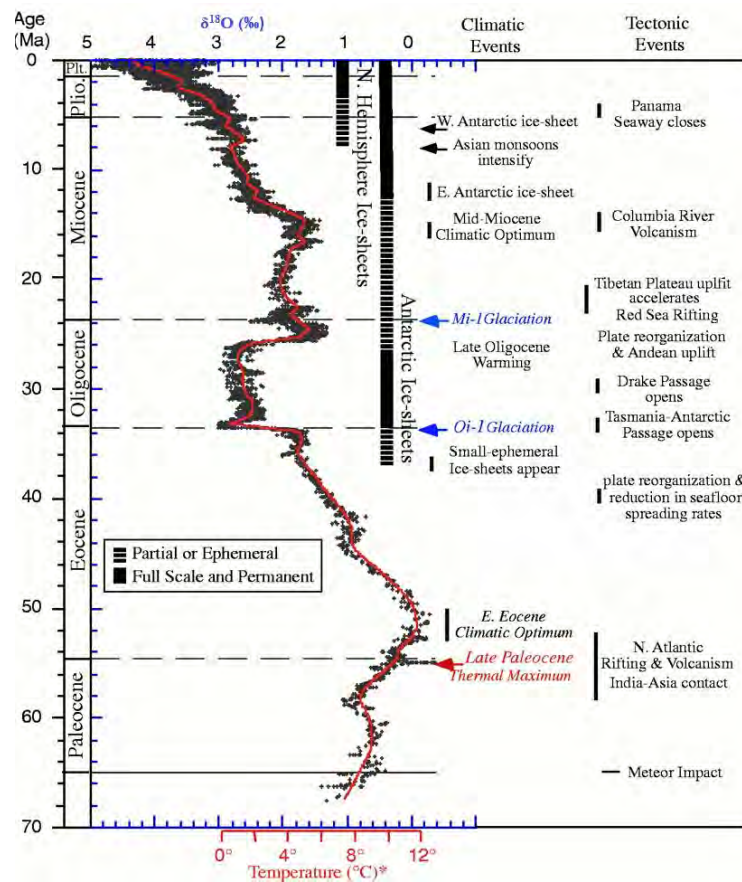


Fig. 1. $\delta^{18}\text{O}$ (‰) de l'océan global basé sur la compilation de plus de 40 sites ODP et DSDP et principaux événements climatiques et tectoniques (modifié d'après Zachos et al., 2001).

Plusieurs facteurs ont pu jouer un rôle dans ces modifications climatiques comme les taux de CO_2 atmosphérique, les paramètres orbitaux, la circulation océanique et les modifications paléogéographiques. Des auteurs ont montré que la variabilité climatique enregistrée durant le Miocène était menée par les fluctuations de l'amplitude de l'obliquité et de l'excentricité de la Terre (Westerhold *et al.* 2005). En revanche, DeConto et Pollard (2003a, b) prônent une combinaison de plusieurs facteurs tels que les variations de CO_2 atmosphérique, les variations orbitales et les feedbacks climatiques. Pendant longtemps on a pensé que la diminution graduelle des taux de CO_2 , due à l'altération des silicates, était le facteur prépondérant (*e.g.* Raymo et al., 1988 ; Raymo et Ruddiman, 1992). Certaines données ont suggéré ensuite que durant le Miocène

les taux de CO₂ étaient similaires, voire inférieurs, aux taux pré-industriels (Pagani et al., 1999; Pearson and Palmer, 2000) mais Kürschner et al. (2008) et plus récemment, Zhang et al. (2013), ont reconstitué, pour les 25 et 40 derniers millions d'années respectivement, des taux de CO₂ plus élevés que les taux précédemment reconstitués. Les taux estimés entre 650-700 ppmv (Kürschner et al., 2008) et 400-500 ppmv (Zhang et al., 2013) sont en accord avec les valeurs seuils du CO₂ établis d'après les simulations climatiques (DeConto et al., 2008) en dessous desquels une glaciation Antarctique (~750 ppmv) ou Arctique (~300 ppmv) peuvent subvenir.

Quoiqu'il en soit, il existe maintenant un consensus grandissant en faveur d'une influence multifactorielle.

La configuration globale des continents était proche de la configuration actuelle dès le Miocène. Cependant, la tectonique des plaques a conduit à des changements paléogéographiques en certains points du globe au cours du Néogène, en particulier durant le Miocène inférieur et moyen. Les plus importants de ces changements paléogéographiques sont l'ouverture de certains passages océaniques (passage de Drake, détroit de Béring) et la fermeture d'autres (fermeture du passage entre océan Atlantique et océan Pacifique à Panama, fermeture du passage entre océan Indien et Tethys) qui ont contribué aux modifications climatiques enregistrées au cours du Néogène (Pagani et al., 2000; Hall et al., 2003). Les changements engendrés sur la circulation océanique ont conduit à l'établissement de son schéma actuel (*e.g.* courant Circumpolaire antarctique) ce qui a largement influencé le climat global.

Par ailleurs, des simulations réalisées par des modèles climatiques ont montré le rôle majeur sur le climat global, via les modifications atmosphériques, de la surrection des chaînes de montagne et hauts plateaux (Alpes, Rocky Mountains, Andes/Altiplano, Himalaya/Tibet) (*e.g.* Ruddiman et Kutzbach 1989; Ramstein et al., 1997; Sepulchre et al., 2006 ; Foster et al., 2010).

Enfin, il est largement admis que la végétation a également une influence significative sur le climat. Des simulations climatiques, mettant en jeu des données de végétation, ont souligné par exemple que la présence de forêts aux hautes de l'hémisphère Nord durant le Néogène, a causé un réchauffement dans les régions polaires et a donc provoqué un gradient latitudinal de température plus plat qu'actuellement (Micheels et al., 2007).

Dans le cadre du réchauffement global que nous connaissons actuellement, nous avons besoin de connaître les mécanismes régissant la variabilité climatique. Une meilleure compréhension des processus mis en jeu dans le passé permettrait donc de mieux prévoir les changements climatiques à venir (notamment leur intensité) et leurs répercussions sur notre environnement. Plusieurs périodes chaudes du passé ont été désignées comme pouvant être des analogues du climat futur (Lunt et al., 2013) : le début de l'Eocène (~55-50 millions d'années (Ma)), le Pliocène moyen (~3.3-3 Ma) et le début du dernier interglaciaire (~130-125 ka) parmi lesquelles le Pliocène moyen semble être le meilleur candidat (Haywood et al., 2013). En effet, avant 5 millions d'années la configuration des continents et des passages océaniques étaient différents de l'actuel ; après 1 million d'années les taux de CO₂ relevés dans les carottes de glace sont toujours inférieurs aux taux pré-industriels (Lüthi et al., 2008). Durant le Pliocène moyen, la paléogéographie, la topographie et la configuration orbitale étaient proches de l'actuel, ce qui en fait la période la plus adéquat.

➡ Afin de participer à l'amélioration de notre connaissance du passé, j'ai choisi, avec le pollen pour bio-indicateur, d'étudier le Cénozoïque afin de mieux comprendre les mécanismes globaux à l'origine des modifications majeures tant au niveau du climat que de la végétation.

Jusqu'à présent, j'ai principalement travaillé sur l'Europe de l'Ouest et plus particulièrement sur la chaîne alpine et la région méditerranéenne car la végétation actuelle de ces régions est très complexe et très hétérogène, la diversité végétale y est très importante. Ces régions sont, en effet, considérées comme des "hot-spots" de diversité à l'échelle du globe (Quézel et Médail, 1995). Par ailleurs, la richesse et la distribution particulière, très fragmentée, des plantes endémiques découlent de toute évidence des bouleversements géologiques (forçages internes) et climatiques (forçages externes) qui ont affecté l'Europe de l'Ouest depuis plus de 40 Ma. La composition et l'organisation de la végétation méditerranéenne et alpine est donc le résultat d'une longue histoire et de multiples influences, notamment de l'hétérogénéité des substrats, de la géomorphologie, du climat et l'isolement des différentes régions (Quézel, 1978, 1985 ; Quézel et al., 1980 ; Quézel et Médail, 2003) : pour comprendre la végétation actuelle d'une région, il faut en étudier son passé. Je me suis donc attachée à reconstituer les paléoclimats et les paléoreliefs de l'Europe occidentale.

Par ailleurs, l'Europe de l'Ouest présente une multitude de dépôts sédimentaires (Fig. 2) du Cénozoïque supérieur (25 derniers Ma) bien datés par biostratigraphie (foraminifères, nannoplancton, mammifères), magnétostratigraphie ou encore cyclostratigraphie. Ces dépôts sont le plus souvent à l'affleurement grâce à l'intense activité tectonique que cette région a connue. Pour la plupart, les données polliniques sont tirées de sédiments marins le plus souvent littoraux, au niveau des paléo-rivages de la Méditerranée miocène et pliocène.

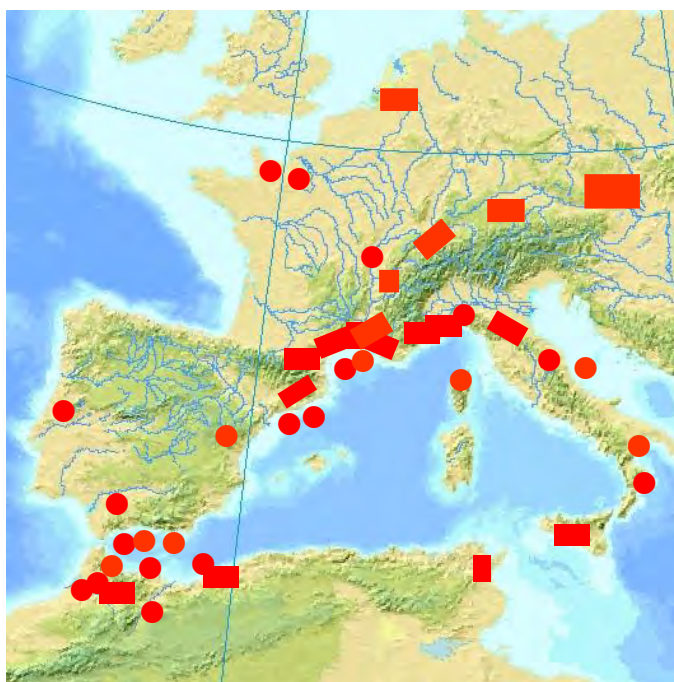


Fig. 2. Flores polliniques couvrant le Néogène (Miocène et Pliocène) en Europe de l'Ouest et région méditerranéenne

Je présenterai dans ce mémoire un bref rappel des méthodes de quantification du climat et des paléoaltitudes qui ont fait leurs preuves sur de nombreuses données polliniques puis je présenterai les principaux résultats que j'ai obtenus, tant au niveau de l'évolution du climat que des paléoaltitudes, deux des principaux moteurs des changements de végétation avant l'apparition de l'Homme.

1 – Méthodes de reconstitution basées sur les données polliniques

1.1. Méthode de reconstitution du climat

Depuis longtemps les scientifiques ont tenté de caractériser le climat à un endroit et une époque donnés sur la base de données paléofloristiques. Le comte de Saporta, paléobotaniste français du 19^{ème} siècle, cherchait déjà à imaginer le climat de l'Europe et de la région méditerranéenne durant le Tertiaire sur la base des plantes fossilisées dans des gisements (Saporta, 1878 ; 1879). En se basant sur la présence de quelques plantes (bananier, laurier rose, laurier, camphrier, palmier par exemple), il donne des valeurs de températures pour différentes périodes géologiques. Toutefois, les informations étaient qualitatives plutôt que quantitatives.

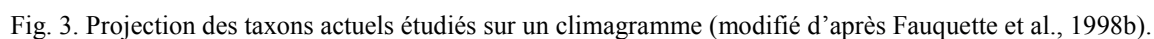
Plus récemment, des méthodes de reconstitution quantitative du climat ont été mises au point, notamment plusieurs méthodes basées sur les amplitudes climatiques supportées par les plantes (Iversen, 1944 ; Grichuk, 1969 ; Mosbrugger et Utescher, 1997). Mais les méthodes décrites sont peu adaptées aux données polliniques car elles ne prennent pas en compte les pourcentages polliniques, simplement le critère de présence/absence.

Pour reconstituer le climat à partir de données polliniques, il existe également la méthode des meilleurs analogues développée par Guiot (1990) et appliquée de nombreuses fois (*e.g.* Guiot et al., 1989, 1992). Cette méthode repose sur la ressemblance des spectres polliniques actuels et fossiles et attribue au spectre fossile le climat du spectre actuel le plus proche dans sa composition. Pour les périodes récentes, d'autres méthodes existent. L'une d'elles, mise au point par Peyron et al. (1998), dérive de la méthode des meilleurs analogues mais est basée sur le concept des types de plante fonctionnels (*PFTs*) et des biomes développée par Prentice et al. (1992). Les *PFTs* sont des groupes de plantes définis par leur taille, forme des feuilles, phénologie et tolérances climatiques. Les biomes sont caractérisés par un ou plusieurs *PFTs*. Les taxons polliniques sont dans un premier temps attribués à un *PFT* puis les *PFTs* sont calibrés en termes de climat. La relation *PFT*-climat est considérée par les auteurs comme étant plus robuste que la relation taxon-climat car les groupes de taxons ont une réponse mieux définie face aux changements du climat que les taxons pris individuellement. L'utilisation des types de plante fonctionnels permet de travailler sur des périodes qui ne connaissent que des analogues partiels de la végétation, par exemple la végétation steppique du dernier maximum glaciaire en Europe (Peyron et al., 1998).

Cependant, ces deux méthodes ne peuvent être appliquées avec succès que sur des périodes récentes car il n'existe de nos jours pas d'environnement végétal qui pourrait fournir des spectres polliniques analogues aux spectres du Néogène et du Paléogène. En effet, les spectres polliniques de ces périodes contiennent en mélange des taxons tempérés, méditerranéens, subtropicaux voire tropicaux dispersés actuellement en Asie, Amérique du Nord, Anatolie, sur les bords de la mer Caspienne.

C'est dans ce contexte que nous avons mis au point une nouvelle méthode du type « méthode des amplitudes climatiques » adaptée aux données polliniques de cette période (Fauquette et al., 1998a, b). Cette méthode est basée sur les amplitudes climatiques supportées par les plantes mais elle a l'avantage de prendre en compte les pourcentages polliniques dans les spectres. En effet, pour la plupart des taxons, nous avons travaillé sur une base de données polliniques actuelles de près de 8000 spectres qui proviennent d'échantillons de surface collectés en Eurasie et Amérique du Nord et compilés par Huntley et Bartlein (*com. pers.*). Cette base de données nous a permis

Par contre, certains des taxons que l'on trouve dans les spectres polliniques du Néogène ne sont pas représentés dans les spectres polliniques actuels de la base de données utilisée. Pour ceux-là, nous avons recherché leurs aires de répartition actuelles et le climat associé à ces aires. Nous avons disposé sur des climagrammes les aires bioclimatiques de certaines plantes en fonction des connaissances de terrain ou des recherches bibliographiques, calées sur les données climatiques régionales correspondantes afin d'obtenir des intervalles climatiques (Fig. 3 ; Fauquette et al., 1998b). C'est à cette occasion que j'ai commencé à travailler avec le Professeur Pierre Quézel, botaniste de l'Université d'Aix-Marseille, spécialiste de la région méditerranéenne *s.l.*, intéressé de longue date par les études paléoécologiques (*e.g.* Quézel, 1989, 1995, 1999 ; Quézel et Barbero, 1993 ; Pons et Quézel, 1998).



Avec toutes ces données en main, pour reconstituer le climat à partir d'un spectre pollinique fossile, il suffit de comparer les exigences climatiques supportées par tous les taxons dépassant leur seuil de présence dans le spectre pollinique. Le climat le plus vraisemblable pour un ensemble de taxons excédant leur seuil de présence/absence et/ou d'abondance est fourni par le plus petit intervalle commun au plus grand nombre de taxons (Fig. 4 ; Fauquette et al., 1998a, b).

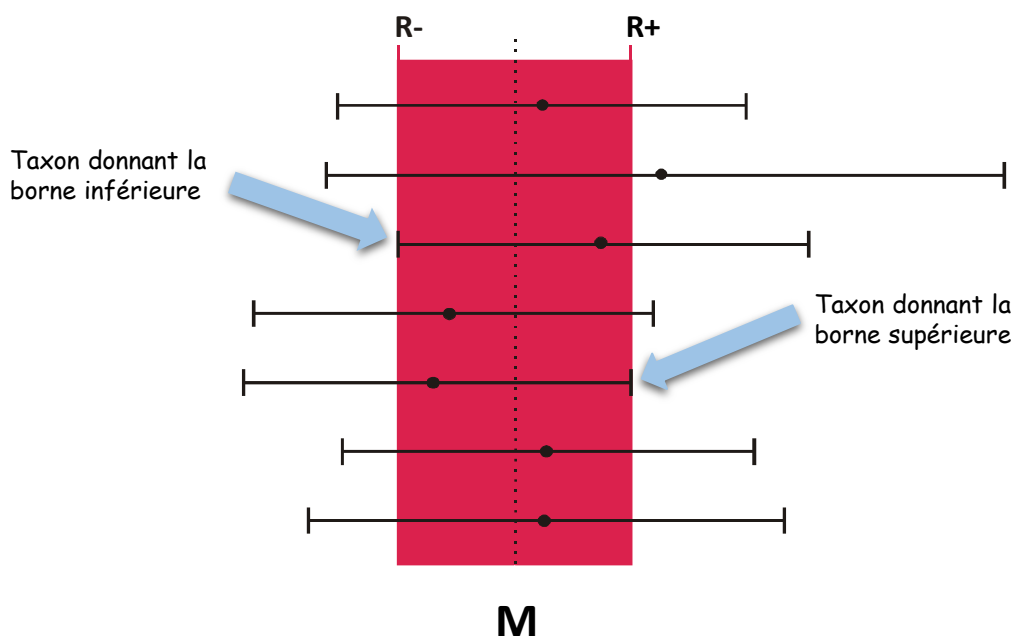


Fig. 4. Superposition des exigences climatiques de plusieurs taxons afin d'en inférer une estimation climatique sous forme d'intervalle $[R- ; R+]$ et d'une valeur moyenne pondérée (Fauquette et al., 1998 a, b).

La base de données regroupant les exigences climatiques des plantes est toujours en évolution avec l'ajout de nouveaux taxons, notamment des taxons tropicaux, qui apparaissent dans les spectres fossiles au fur et à mesure des nouvelles périodes ou des nouvelles régions étudiées.

Bien sûr, comme pour toutes les méthodes, la méthode des amplitudes climatiques a des limites :

- 1 Notre hypothèse de base concernant les taxons ne peut être que l'écologie des plantes était la même qu'actuellement ;
- 2 les aires de répartition actuelles ont été modifiées par l'homme ;
- 3 problèmes de transport et/ou de conservation des grains de pollen ;
- 4 les intervalles reconstitués sont souvent très larges. Ceci est dû à la plasticité relative des plantes et au fait que l'on travaille au niveau du genre ou de la famille des plantes, rarement au niveau de l'espèce. D'un autre côté, cela permet de contre balancer le point n°2.

On peut donc se poser 2 questions primordiales : jusqu'à quelle époque peut-on remonter ? Est-ce que les exigences climatiques des plantes ont varié dans le temps ?

Les nombreuses études palynologiques portant sur le Néogène (*e.g.* Roche et Schuler, 1976; Bessedik et al., 1984 ; Bessedik, 1985; Suc, 1989; Zheng, 1990; Suc et al., 1995a, b, c, 1999; Jiménez-Moreno, 2005; Bertini et Martinetto, 2011) ont montré que la végétation européenne à cette époque suivait une zonation latitudinale et un étagement altitudinal similaire à la répartition actuelle dans le Sud-Est de la Chine (Wang, 1961) où la plupart des taxons qui ont disparu d'Europe à la fin du Néogène sont encore présents. Cela nous permet donc d'avoir un contrôle sur les estimations climatiques obtenues. Néanmoins, il faudra dans un futur proche répondre à ces 2 questions afin d'être sûr des résultats avancés.

1.2. Méthode de reconstitution des paléoaltitudes

Une grande part de mon travail durant ces années s'est focalisée sur la reconstitution des paléoaltitudes de certains massifs montagneux à partir des données polliniques et climatiques. Depuis longtemps la reconstitution des paléoaltitudes intéresse les géologues, pour qui toute information permettant de préciser l'âge de la formation des reliefs ainsi leur altitude est de première importance pour retracer les événements orogéniques et l'ampleur des processus d'érosion. Mais la géologie seule ne permet pas toujours de connaître précisément ni les dates de mise en place des reliefs ni les altitudes.

Ces reconstitutions intéressent également les modélisateurs du climat afin d'affiner les conditions d'entrées des modèles de circulation générale.

Il s'avère que la palynologie est un très bon outil pour reconstituer les paléoaltitudes car les bassins sédimentaires reçoivent avec les particules terrigènes apportées par les fleuves des grains de pollen en grande quantité, représentatifs de tous les étages de végétation du bassin versant. L'expérience acquise sur les sédiments actuels du Rhône (Beaudouin et al., 2005) a montré que l'on pouvait utiliser l'étage de végétation arborée le plus élevé pour apprécier l'altitude minimale des reliefs avoisinants.

Le principe de base réside sur le fait que les étages de végétation de l'hémisphère Nord s'élèvent régulièrement en fonction de la diminution de la latitude (Fig. 5 ; Troll, 1973). Bien sûr, l'étagement vertical de la végétation avec la latitude est évident mais difficile à quantifier car la répartition altitudinale des végétaux dépend de nombreux paramètres climatiques mais également de conditions locales comme la nature des sols, l'orientation de la pente par exemple.

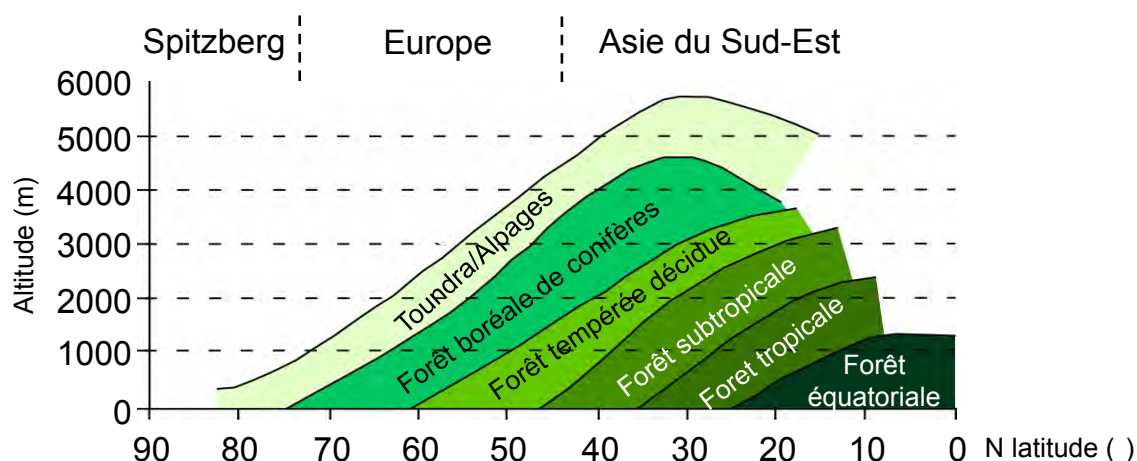


Fig. 5. Répartition en altitude des groupements végétaux en fonction de la latitude (d'après Troll, 1973).

Toutefois, à grande échelle, on sait qu'un même étage de végétation se trouve à des altitudes différentes si les massifs ne sont pas à la même latitude. Si on regarde la répartition du hêtre (Ozenda, 1989) ou de l'étage à sapin et épicéa (Noirfalise et al., 1987 ; Ozenda, 1961) en altitude en fonction de la latitude, on voit que la relation est quasi-linéaire (Fig. 6) et peut être estimée à environ 110 m en altitude pour 1 degré de latitude (Ozenda, 1989).

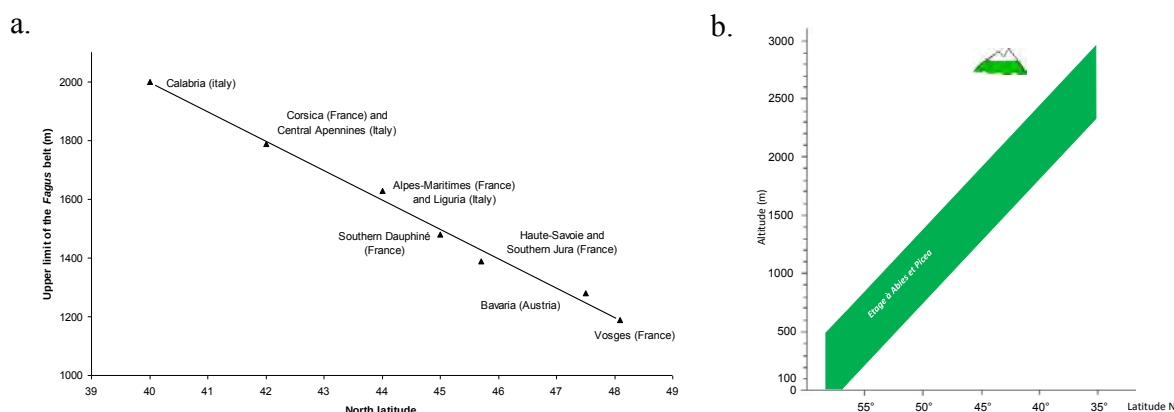


Fig. 6. Variation altitudinale de l'étage du hêtre (a) et du sapin/épicéa (b) en fonction de la latitude en Europe de l'Ouest.

Le calcul de l'altitude minimale du massif le plus proche du site pollinique passe par le calcul de la paléo-température moyenne annuelle au niveau de la mer grâce à la méthode des amplitudes climatiques (Fauquette et al., 1998a, b). Dans un deuxième temps, après usage d'un gradient thermique altitudinal/latitudinal ($\sim 0.60^{\circ}\text{C}$ par degré de latitude et $\sim 0.55^{\circ}\text{C}$ par 100 m en altitude, Ozenda, 1989) et de l'étagement altitudinal actuel des arbres microthermes (c'est-à-dire supportant des conditions boréales), nous pouvons déterminer l'altitude passée de l'étage arboré le plus élevé (généralement l'étage à sapin et épicéa), par conséquent l'altitude minimale du massif (Fauquette et al., 1999b). Ainsi, ces restitutions peuvent-elles fournir un suivi temporel de la surrection des zones étudiées.

Les valeurs estimées sont des valeurs minimales car les données polliniques ne permettent pas d'établir l'amplitude de l'étage à sapin et épicéa, ni de savoir si un étage alpin herbacé ou un étage nival existaient au-dessus.

Pour des bassins continentaux, d'altitude à priori inconnue, il a fallu mettre au point une autre méthode afin de reconstituer les paléoaltitudes au cours du temps (Suc et Fauquette, 2012). Cette méthode demande de calculer la température annuelle du bassin continental (t_1) et d'un site de même âge situé au niveau de la mer (t_2). La différence de latitude entre les 2 sites étant connue (DI), on utilise le gradient latitudinal de température pour déduire la température du site continental s'il était à basse altitude (t_3). La différence entre t_1 et t_3 correspond à l'effet de l'altitude sur la température du site continental. En utilisant le gradient altitudinal de température, on peut alors en déduire la paléoélévation du site continental (Pe) (Fig. 7).

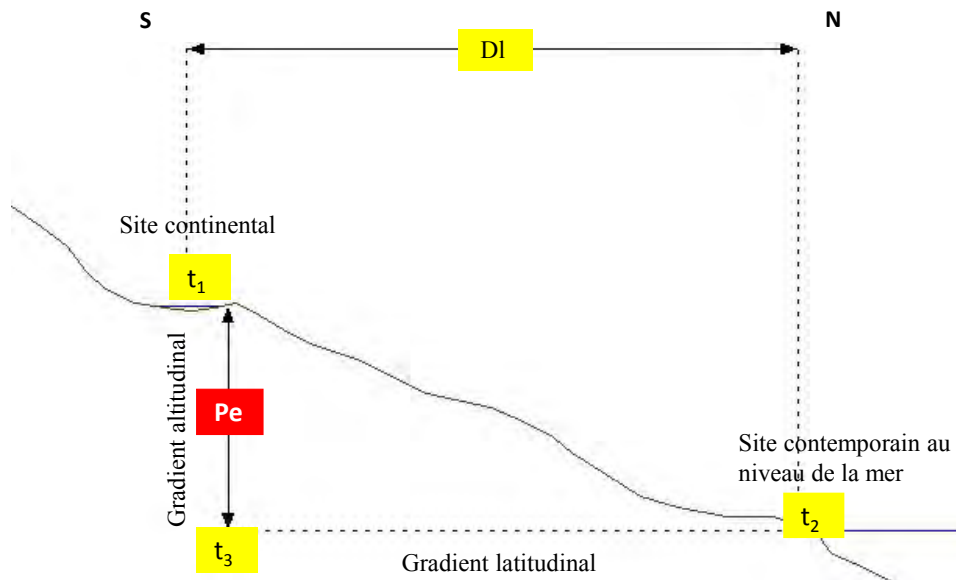


Fig. 7. Méthode de reconstitution de la paléoélévation d'un site continental (modifié d'après Suc et Fauquette, 2012).

2 – Modifications majeures du climat en Europe de l'Ouest et Méditerranée depuis l'Oligocène

Le climat est un des moteurs des modifications de la végétation au cours du temps. Il est donc nécessaire, afin de comprendre les patrons actuels de la diversité végétale et de la distribution des plantes en Europe de l'Ouest et en région méditerranéenne, de connaître les grands changements climatiques au cours du temps.

J'ai choisi dans ce mémoire de présenter les modifications du gradient climatique latitudinal, la problématique du gradient altitudinal et les changements climatiques lors des premiers cycles glaciaire/interglaciaire de l'hémisphère Nord.

2.1. Variations des gradients climatiques

2.1.1. Le gradient latitudinal

L'origine de cette étude réside dans le fait que les données polliniques du Néogène laissent entrevoir l'existence d'un climat chaud et humide au Nord-Ouest de la Méditerranée mais chaud et sec au Sud-Ouest de la Méditerranée (Suc, 1989 ; Suc et al., 1995a), avec toutefois des variations au cours du temps.

Afin de confirmer ce constat et de donner des valeurs quantifiées, j'ai réalisé une série de reconstitutions afin de retracer l'évolution du gradient climatique latitudinal dans le temps, depuis l'Oligocène inférieur (Rupélien) jusqu'au Pliocène moyen (Plaisancien) en Europe de l'Ouest et la région méditerranéenne (Fauquette et al., 2007, 2015).

Pour le Rupélien (34-28 Ma), le gradient a été calculé à partir des données polliniques du site de Tongres en Belgique (50°46'N, Roche et Schuler, 1976) et du site de Montauban (Fig. 8 ; France, 44°01'N, Fauquette et al., 2015).

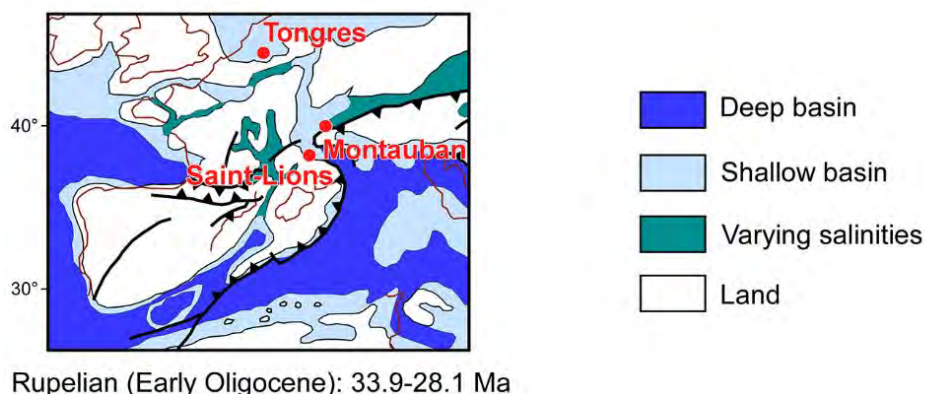


Fig. 8. Localisation des sites de Tongres et Montauban (carte paléogéographique de Meulenkamp et Sissingh, 2003).

Les températures annuelles (T_a) sont respectivement de 17.5°C et 19.6°C pour un décalage en latitude de 4.5° à cette époque (Fig. 8 ; Meulenkamp et Sissingh, 2003). Cela indique donc un gradient thermique latitudinal d'environ 0.46°C par degré de latitude à cette époque, contre environ 0.6°C par degré de latitude actuellement.

Pour le Miocène moyen (~15 Ma), notamment grâce aux travaux de G. Jiménez-Moreno que j'ai co-encadré en thèse, les données polliniques sont plus nombreuses (Fig. 9a ; Jiménez-Moreno, 2005 ; Jiménez-Moreno et al., 2010 ; Fauquette et al., 2007), ce qui permet de percevoir le patron climatique dans cette région (Fig. 9b ; Fauquette et al., 2007) : les températures annuelles étaient plus élevées qu'actuellement dans toute la région (T_a 2 à 6°C plus élevées), en particulier vers le Nord (T_a 8°C plus élevées), et les précipitations étaient plus importantes qu'actuellement en région nord-ouest méditerranéenne (P_a 200 à 700 mm de plus) mais équivalentes à l'actuel en région sud-ouest méditerranéenne.

Sur la base de ces reconstitutions climatiques, le gradient thermique pour le Miocène moyen est estimé à environ 0.48°C par degré de latitude (Fauquette et al., 2007).

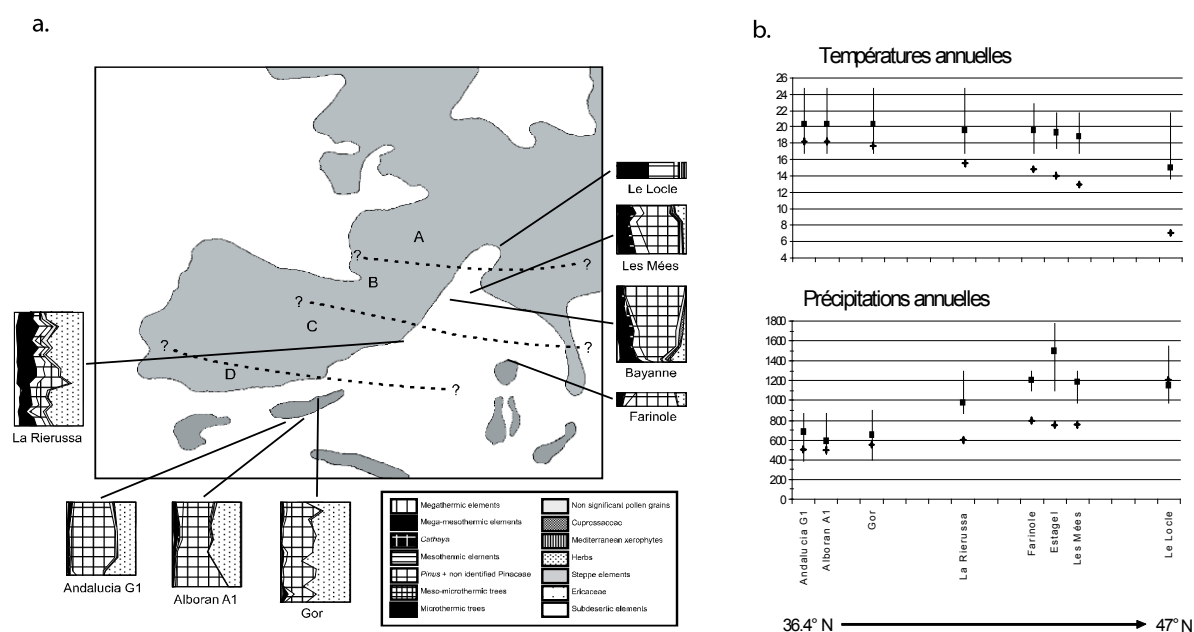


Fig. 9. a. Données polliniques du Miocène moyen (~15 Ma) dans le Sud-Ouest de l'Europe (d'après Jiménez-Moreno, 2005 ; Jiménez-Moreno et al., 2010 ; Fauquette et al., 2007). Carte paléogéographique du début de Serravallien d'après Rögl (1998). b. Reconstitution des températures et précipitations annuelles (Fauquette et al., 2007).

Pendant le Tortonien (~10 Ma), les données polliniques (Fig. 10a) indiquent que le climat était chaud et humide dans l'Ouest de l'Europe (Fig. 10b ; Ta 4 à 9°C et Pa de 100 à 600 mm de plus qu'actuellement) et chaud et sec dans la région Sud-Méditerranéenne (Fig. 9b ; Ta 3 à 4°C et Pa 150 mm de plus qu'actuellement). Le gradient latitudinal climatique au Tortonien était semblable à l'actuel. Sur la base des estimations de la température annuelle dans le Nord du Maroc (MSD1) et d'Ambérieu en France (Fig. 10b), on peut reconstituer un gradient thermique d'environ 0.6°C par degré de latitude (Fauquette et al., 2007).

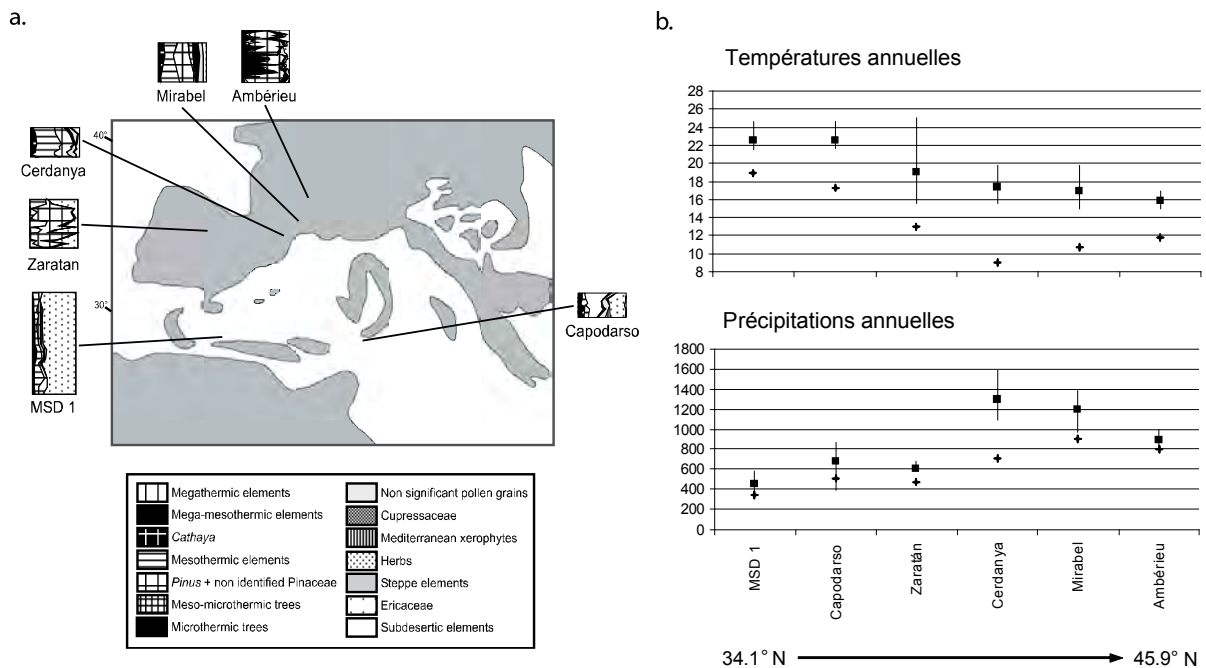


Fig. 10. a. Données polliniques du Tortonien (~10 Ma) dans le Sud-Ouest de l'Europe (d'après Jiménez-Moreno et al., 2010 ; Fauquette et al., 2007). Carte paléogéographique du Tortonien d'après Paramonova (2004). b. Reconstitution des températures et précipitations annuelles (Fauquette et al., 2007).

Au Pliocène inférieur (~5.3 Ma) et au Pliocène moyen (~3.5 Ma), le climat était chaud et humide au Nord-Ouest de la Méditerranée (1 à 4°C et 400 à 700 mm de plus qu'actuellement) mais chaud et sec au Sud-Ouest de la Méditerranée (1 à 5°C de plus qu'actuellement et aussi sec voire plus sec qu'actuellement) (Figs. 11 et 12). Le gradient thermique a été estimé à environ 0.6°C par degré de latitude pour le Pliocène inférieur et moyen (Fauquette et al., 1999a, 2007).

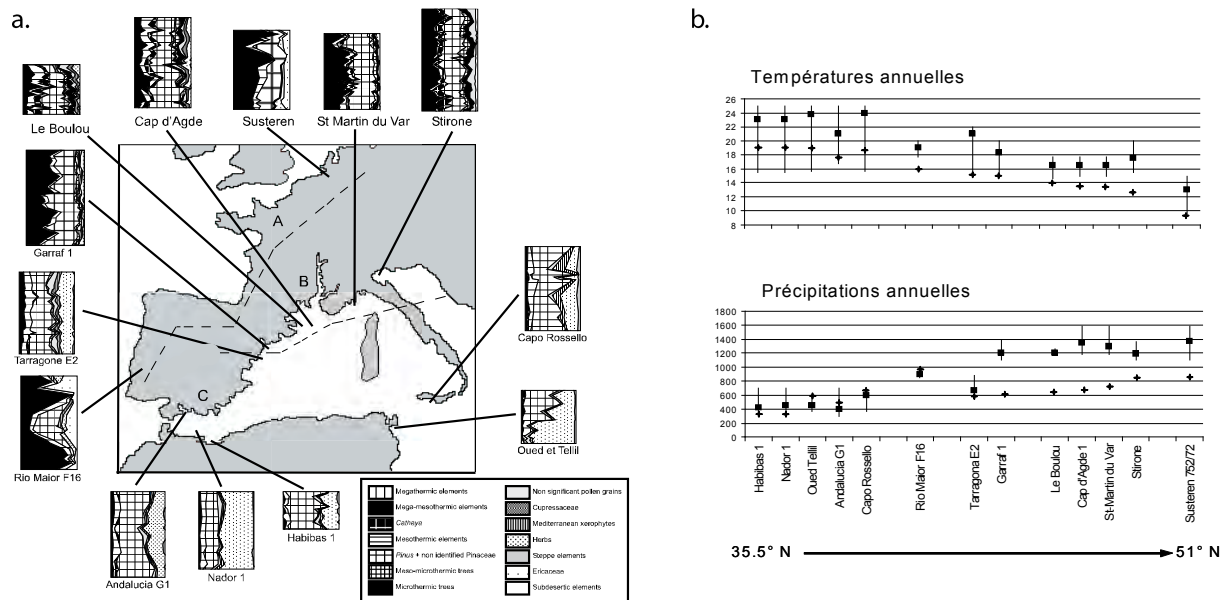


Fig. 11. a. Diagrammes polliniques du Pliocène inférieur (~ 5-5.3 Ma) dans le Sud-Ouest de l'Europe (d'après Fauquette et al., 2007). Carte paléogéographique du Pliocène inférieur (Clauzon et al., 1995 ; Clauzon, 1996 ; Jolivet et al., 2006). b. Reconstitution des températures et précipitations annuelles (Fauquette et al., 1999b, 2007). Localités polliniques : Susteren 752/72 (Zagwijn, 1960), Saint-Martin du Var (Zheng, 1990), Stirone (Bertini, 1994, 2001), Cap d'Agde 1 (Suc, 1989), Rio Maior F16 (Diniz, 1984), Andaluçia G1 (Suc *et al.*, 1995a), Le Boulou (Suc *et al.*, 1999), Nador 1 (Fauquette *et al.*, 1999a), Habibas 1 (Suc *et al.*, 1999), Tarragone E2 (Bessais et Cravatte, 1988), Garraf 1 (Suc et Cravatte, 1982), Qued et Tellil (Suc *et al.*, 1999), Capo Rossello (Suc *et al.*, 1995c).

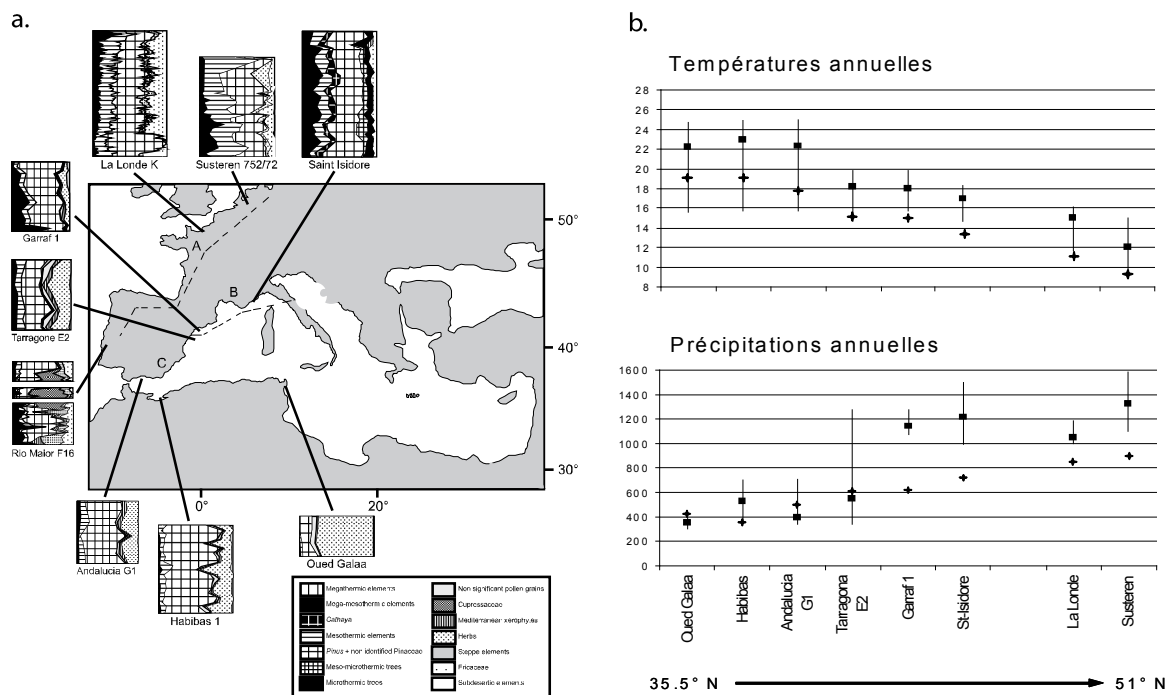


Fig. 12. a. Diagrammes polliniques du Pliocène moyen (~ 3.5-3 Ma) dans le Sud-Ouest de l'Europe (d'après Fauquette et al., 2007). Carte paléogéographique du Pliocène moyen (Khondkarian et al., 2004). b. Reconstitution des températures et précipitations annuelles (Fauquette et al., 1999b, 2007). Localités polliniques : Susteren 752/72 (Zagwijn, 1960), La Londe (Clet et Huault, 1987), Saint-Isidore du Var (Zheng, 1990), Garraf 1 (Suc et Cravatte, 1982), Tarragone E2 (Bessais et Cravatte, 1988), Andaluçia G1 (Suc *et al.*, 1995a), Qued Galaa (Suc unpublished), Rio Maior F16 (Diniz, 1984).

Pour le Pliocène, il est aisé de superposer (Fig. 13) les valeurs climatiques obtenues d'après les données polliniques et les valeurs climatiques actuelles correspondant aux grands ensembles de végétation de la façade Ouest des Etats-Unis (Walter, 1979), en particulier la Californie dont l'organisation de la végétation peut être comparée à celle du Pliocène méditerranéen (Axelrod, 1973).

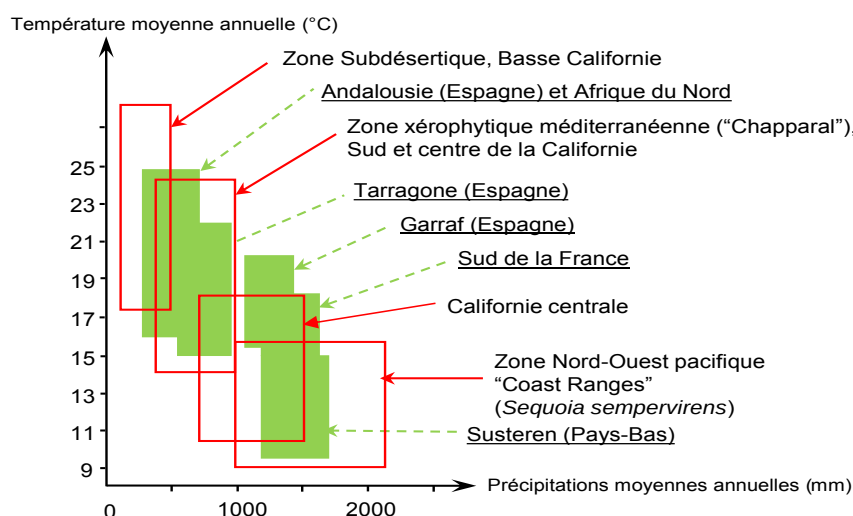


Fig. 13. Comparaison des grandes structures de végétation de Californie (rectangles rouges) et du Pliocène méditerranéen (rectangles verts) (modifié d'après Fauquette et al., 2007).

Par ailleurs, la reconstitution du gradient thermique latitudinal en Europe de l'Ouest au Pliocène est en accord avec la simulation climatique réalisée à l'aide du modèle LMDz (Fig. 14 ; Jost 2005 ; Jost et al., 2009 ; Fauquette et al., 2007) qui met en évidence dans notre zone d'étude le parallèle entre gradient actuel et gradient pliocène, bien que les températures soient plus basses de nos jours.

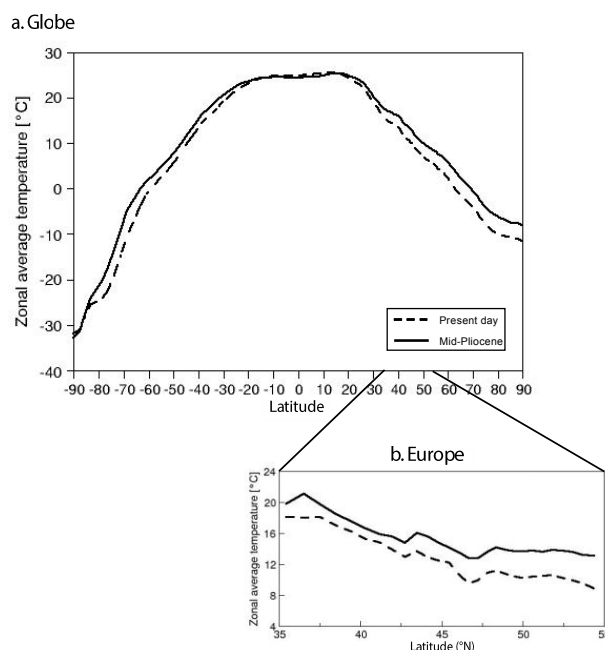


Fig. 14. Températures moyennes annuelles sur les continents simulées par le modèle LMDz pour le Pliocène moyen (trait plein) et l'actuel (pointillé), a) pour le globe, b) pour l'Europe (Jost, 2005 ; Fauquette et al., 2007).

De la même façon, la simulation réalisée par Haywood et al. (2000a) avec le modèle UKMO (*UK Meteorological Office*) est en accord avec notre reconstitution du gradient latitudinal de précipitation puisqu'ils mettent également en évidence des précipitations plus importantes qu'actuellement en Europe, jusqu'à environ 40°N, et des valeurs proches de l'actuel plus au sud (Fig. 15).

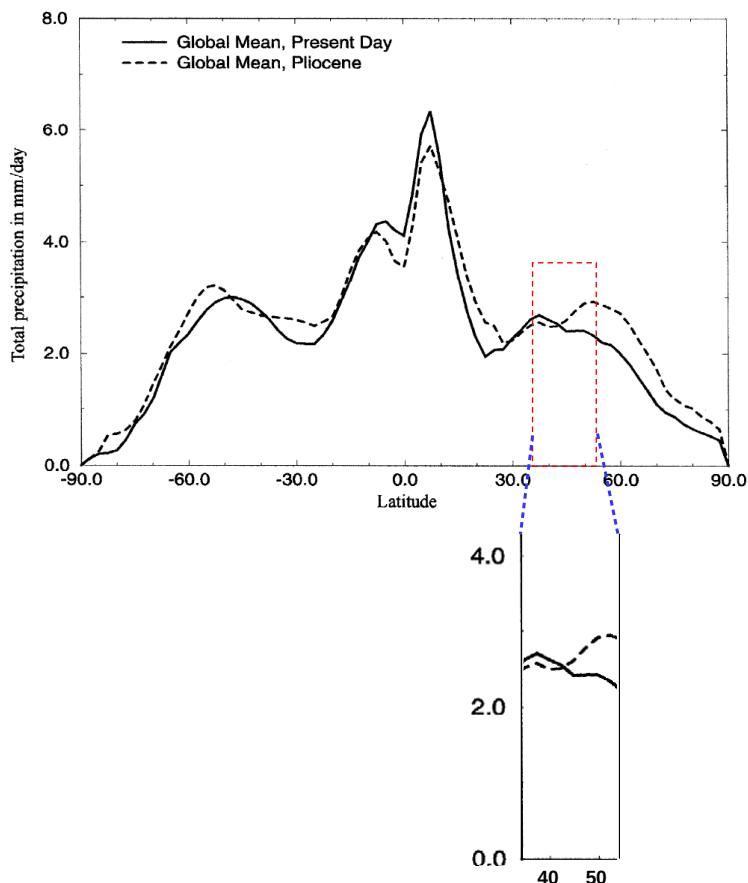


Fig. 15. Précipitations annuelles simulées par le modèle UKMO (UK Meteorological Office) pour le Pliocène moyen (pointillés) et l'actuel (trait plein) pour le globe (Haywood et al., 2000a).

Nos résultats concordent bien également avec les mécanismes climatiques décrits par les simulations réalisées par Haywood et al. (2000b) pour le Pliocène moyen grâce au modèle HadAM3 de l'office météorologique du Royaume-Uni. Ce modèle explique le patron climatique du Pliocène par la faible quantité de glace sur le Groenland (donnée d'entrée du modèle : 50% de glace en moins), des températures des eaux de surface plus élevées en Atlantique Nord (Dowsett et al., 1999), l'anticyclone des Açores et la dépression Nord-Atlantique renforcés. Cela a pour conséquence une intensification des vents d'Ouest, qui, combinée avec des eaux de surface Nord-Atlantiques chaudes, conduit à une augmentation de l'apport de chaleur atmosphérique et d'humidité sur l'Europe et le Nord de la Méditerranée (Fig. 16 ; Haywood et al., 2000b). Ce qui valide mes reconstitutions.

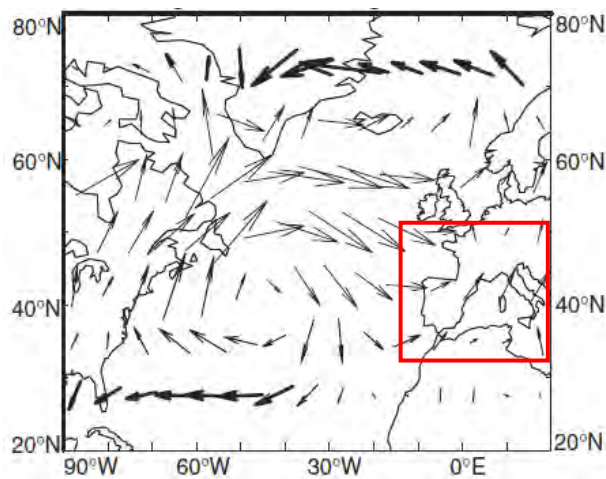


Fig. 16. Vecteurs des vents de surface en Atlantique Nord simulés par le modèle HadAM3 de l'office de météorologie du Royaume-Uni pour le Pliocène Moyen (~3 Ma ; Haywood et al., 2000b).

En conclusion, tous les résultats obtenus, de l'Oligocène inférieur au Pliocène moyen, confirment donc l'existence, comme subodoré dans les données polliniques, d'un gradient thermique croissant du nord vers le sud et un gradient de précipitation décroissant du nord vers le sud. Par contre, il apparaît nettement que ce gradient se modifie au cours du temps : le passage d'un faible gradient thermique au gradient actuel aurait eu lieu juste avant ou durant le Tortonien.

En ce qui concerne le gradient de précipitation, il est plus accusé au Néogène qu'actuellement. Le passage au gradient actuel a donc certainement eu lieu au Pléistocène inférieur, durant les premiers cycles glaciaire-interglaciaire de l'hémisphère nord.

2.1.2. Problématique du gradient altitudinal

Ces reconstitutions spatiales nous ont bien sûr amené sur la problématique du gradient thermique altitudinal dans le passé.

En effet, la méthode développée par Fauquette *et al.* (1999b) pour quantifier les paléoaltitudes est, comme nous l'avons vu, basée sur des données polliniques réalisées à partir de sédiments marins littoraux, ce qui permet d'obtenir une image régionale de la végétation, depuis le littoral, jusqu'aux hautes altitudes du bassin versant. Le calcul de l'altitude minimale du massif le plus proche du site pollinique passe par le calcul de la paléotempérature moyenne annuelle au niveau de la mer et l'usage des gradients thermiques altitudinal/latitudinal.

Nous connaissons maintenant les valeurs du gradient latitudinal pour différentes périodes mais, comme les données polliniques ne permettent pas de connaître le gradient thermique altitudinal passé, en première approximation, j'ai toujours utilisé la relation standard établie entre gradient altitudinal et latitudinal par Ozenda (2002) qui indique que les étages de végétation montent de 110 m en altitude par degré de latitude vers le Sud pour compenser les températures plus élevées.

Il est évident que le gradient altitudinal est très variable en fonction notamment de la pente, la direction des vents, la continentalité et la composition atmosphérique. Meyer (1992) a mis en évidence des gradients actuels compris entre 0.36 et 0.81°C/100 m en différentes régions du globe. Est-il donc transposable dans le passé (Spicer, sous presse) ?

Mes estimations de paléoaltitude sont basées sur l'hypothèse que la relation entre les deux gradients était la même qu'actuellement. Toutefois, si on tenait compte des reconstitutions de

gradients latitudinaux et de l'amplitude des valeurs du gradient altitudinal actuel, la relation serait différente et conduirait à des estimations différentes des paléoaltitudes. Par contre, si on émet l'hypothèse de la conservation dans le temps du ratio entre les deux gradients, les valeurs du gradient thermique altitudinal restent dans la fourchette donnée par Meyer (1992) (Tab. 1).

	Gradient latitudinal (°C/° lat)	Gradient thermique altitudinal (°C/100 m)	Déplacement en altitude/° en latitude
Actuel	0.6	0.55	1° lat → 110 m altitude
Pliocène	0.6	0.36	1° lat → 167 m altitude
		0.55	1° lat → 110 m altitude
		0.8	1° lat → 75 m altitude
Miocène moyen	0.48	0.36	1° lat → 134 m altitude
		0.55	1° lat → 87 m altitude
		0.8	1° lat → 60 m altitude
		0.44	1° lat → 110 m altitude
Oligocène inférieur	0.46	0.36	1° lat → 128 m altitude
		0.55	1° lat → 84 m altitude
		0.8	1° lat → 57 m altitude
		0.42	1° lat → 110 m altitude

Tableau 1. Déplacements en altitude des étages de végétation en fonction des gradients latitudinaux reconstitués et de différentes valeurs du gradient thermique altitudinal : le minimum (0.36°C/100 m) et le maximum (0.8°C/100 m) calculés par Meyer (1992) pour différentes régions du globe, l'actuel dans les Alpes (0.55°C/100 m). Les valeurs en gras correspondent au gradient altitudinal estimé si on émet l'hypothèse de la conservation dans le temps de la relation entre les 2 gradients (d'après Fauquette et al., sous presse).

De plus, pour compenser l'utilisation du ratio altitudinal/latitudinal actuel, je reconstitue les paléoaltitudes à partir non seulement de la valeur moyenne des températures annuelles estimées mais également de l'intervalle complet. Par ailleurs, les reconstitutions de paléoaltitudes déjà réalisées sont cohérentes avec les reconstitutions géomorphologiques ou tectoniques (Fauquette et al., 1999b ; Melinte-Dobrinescu et al., 2009 ; Suc et Fauquette, 2012).

Le temps de la réflexion était venu car ces incertitudes sur les paléo-gradients posaient beaucoup de questions qui auraient pu remettre en cause les résultats déjà acquis.

2.2. Premiers cycles glaciaire/interglaciaire de l'hémisphère Nord

Un moment-clé de l'histoire climatique du Néogène correspond au début du Pléistocène avec la mise en place des premiers cycles glaciaire/interglaciaire de l'hémisphère Nord à ~ 2.6 Ma.

La reconstitution du climat sur les données polliniques de Garraf (Fauquette et al., 1998a) avait mis en évidence un climat chaud et humide sur la plus grande partie de la séquence puis un climat oscillant à partir de la mise en place des cycles glaciaire/interglaciaire. Pendant les phases glaciaires, le climat était plus frais et plus sec qu'auparavant, puis, pendant les phases interglaciaires, le climat revenait au niveau du climat du début du Pliocène.

De la même façon, une quantification paléoclimatique a été réalisée sur le Pliocène de la plaine du Pô (coupe de Stirone) (Fauquette et Bertini, 2003). Cette étude a notamment permis de quantifier les variations climatiques dans cette région au moment des premiers cycles glaciaire-interglaciaire de l'hémisphère Nord. Les résultats ont montré que dans cette région, au début du

Pliocène et durant les phases interglaciaires, le climat était chaud et humide (températures moyennes annuelles de 16 à 20°C, précipitations moyennes annuelles de 1100 à 1500 mm), comme pour toute la région nord-ouest Méditerranéenne. Par contre, durant les phases glaciaires, le climat présentait deux particularités par rapport aux autres sites méditerranéens : la température annuelle et la température du mois le plus chaud étaient plus basses que durant le Pliocène inférieur mais les précipitations annuelles et la température du mois le plus froid diminuait peu, ce qui permettait la persistance d'un environnement forestier. Le schéma classique de ces premiers cycles (alternance steppe/forêt), n'était pas reproduit dans cette région. La Plaine du Pô était donc, au moment des premiers cycles glaciaire-interglaciaire, une région très particulière d'un point de vue végétation et climat.

Une troisième étude a été réalisée à partir la séquence pollinique haute résolution de Semaforo (Italie du Sud) couvrant la période comprise entre 2.46 et 2.11 millions d'années (Combourieu-Nebout, 1993). Les résultats de la quantification climatique (Klotz, Fauquette et al., 2006) obtenus grâce à la méthode des *Probability mutual Climatic Spheres* (PCS, une méthode du type « amplitudes climatiques » développée par Klotz, 1999) nous ont permis de mettre en évidence plusieurs traits d'évolution du climat le long de 9 cycles glaciaire/interglaciaire. Nos reconstitutions révèlent des températures et des précipitations plus importantes qu'aujourd'hui durant les périodes interglaciaires (Ta ~3°C de plus et Pa 500 mm de plus qu'actuellement), suggérant des conditions subtropicales humides. Durant les glaciaires, les températures étaient équivalentes ou plus basses qu'actuellement et les précipitations étaient comparables à l'actuel (Fig. 17).

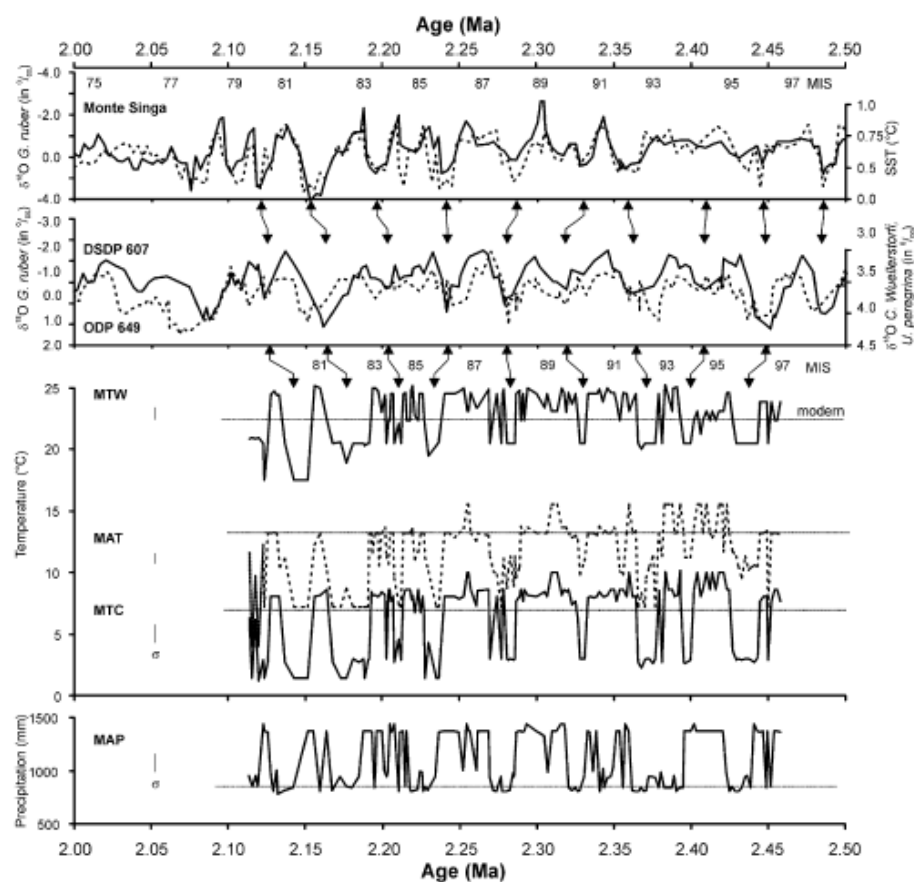


Fig. 17. Reconstitution du climat régional entre 2.46 et 2.11 Ma (Pléistocène inférieur) dans la région de Crotona (d'après Klotz et al., 2006).

Notre étude est cruciale car elle permet de mettre clairement en évidence une tendance à la réduction des températures annuelles et d'hiver ainsi qu'une saisonnalité plus marquée le long des interglaciaires consécutifs et une importante diminution des températures annuelle, hivernale mais également estivale le long des glaciaires consécutifs. Enfin, au moment des transitions interglaciaire-glaciaire, les amplitudes climatiques (différence entre la valeur de l'interglaciaire et la valeur du glaciaire successif) augmentent progressivement du plus ancien cycle au plus récent enregistré dans la section de Semaforo (Fig. 18).

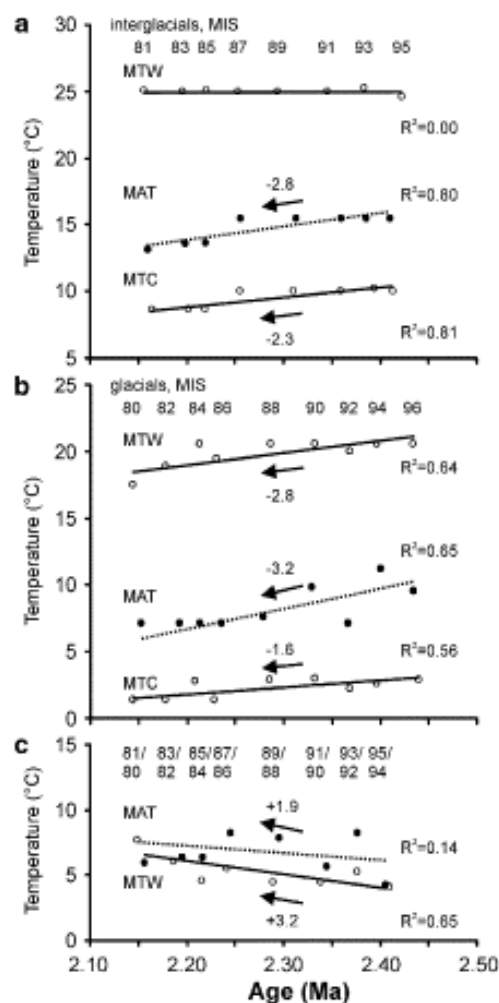


Fig. 18. Tendances climatiques (températures du mois le plus chaud, MTW, annuelles, MAT, du mois le plus froid, MTC) (a) le long des interglaciaires consécutifs et (b) les glaciaires consécutifs à Semaforo. (c) amplitudes thermiques aux transitions interglaciaire/glaciaire (Klotz et al., 2006).

A ces grandes modifications du climat depuis environ 35 millions d'années qui ont modelé en partie la végétation de l'Europe du Sud-Ouest et de la région méditerranéenne, s'ajoutent des contraintes géologiques majeures qui, elles aussi, ont influencé l'histoire de la végétation.

3 – Modifications majeures des paléoreliefs en Europe depuis l'Oligocène.

Mon travail s'est jusqu'à présent principalement focalisé sur la région méditerranéenne au sens large et sur le massif alpin. En effet, pour comprendre la végétation actuelle de cette région, un des "hot-spots" de diversité à l'échelle du globe, avec environ 2000 espèces pour 15000 km² (Quézel et Médail, 1995), il faut en étudier son passé. La richesse et la distribution particulière, très fragmentée, des plantes endémiques découlent de toute évidence des bouleversements géologiques (forçages internes) et climatiques (forçages externes) qui ont affecté la région depuis plus de 40 millions d'années. La composition et l'organisation de la végétation méditerranéenne et alpine est donc le résultat d'une longue histoire et de multiples influences, notamment de l'hétérogénéité des substrats, de la géomorphologie, du climat et l'isolement des différentes régions (Quézel, 1978, 1985 ; Quézel et al., 1980 ; Quézel et Médail, 2003).

Il fallait donc pour comprendre cette particularité étudier, en plus des grandes tendances climatiques, l'évolution de la paléogéographie et de la topographie des différents massifs de cette région au cours du temps (Fig. 19). Par contre, pour un massif donné, nous n'avons pas toujours de sédiments suffisamment anciens pour connaître la date de soulèvement.

C'est le cas par exemple des Apennins du Sud ou des Pyrénées-Orientales pour lesquels les enregistrements polliniques ne démarrent qu'après que les massifs aient été soulevés (Fig. 19).

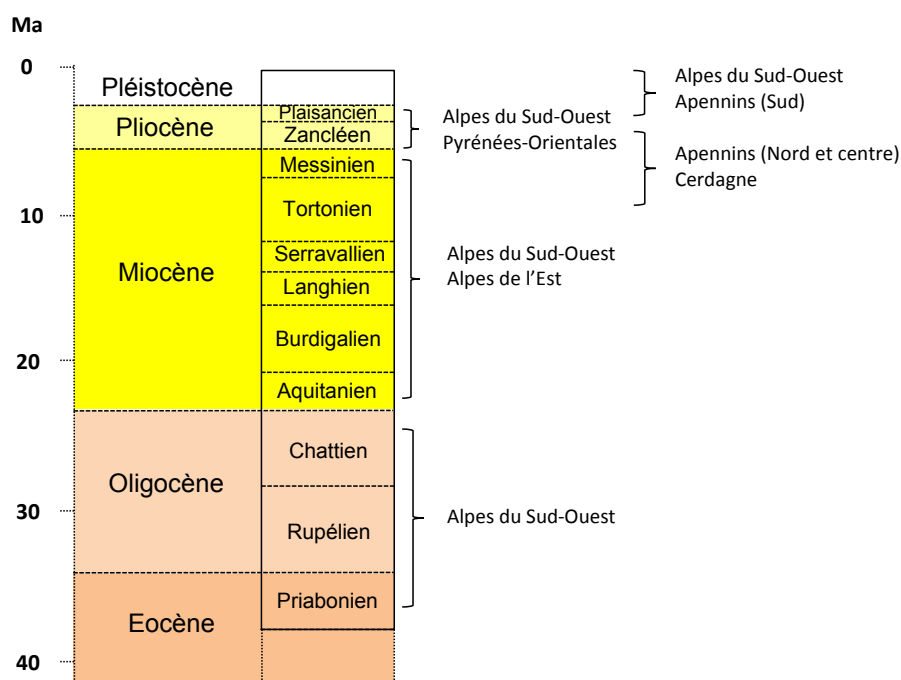


Fig. 19. Chronostratigraphie et régions étudiées.

3.1. Eocène/Oligocène

Peu de données polliniques sont disponibles pour la fin du Paléogène. Sur la bordure Sud-Est du massif alpin, nous avons les données de Gassin Torinese (Bartonien, ~37-38 Ma) sur les collines de Turin, sur la bordure Sud-Ouest, les données de Saint-Lions (Rupélien, ~30 Ma) et

Gambi (Chattien, ~26 Ma) dans le bassin de Barrême et sur la bordure Nord-Ouest, les données de Montauban (Rupélien, ~30 Ma) proche du lac Léman, au pied du Mont-Blanc (Fig. 20; Fauquette et al., 2015a).

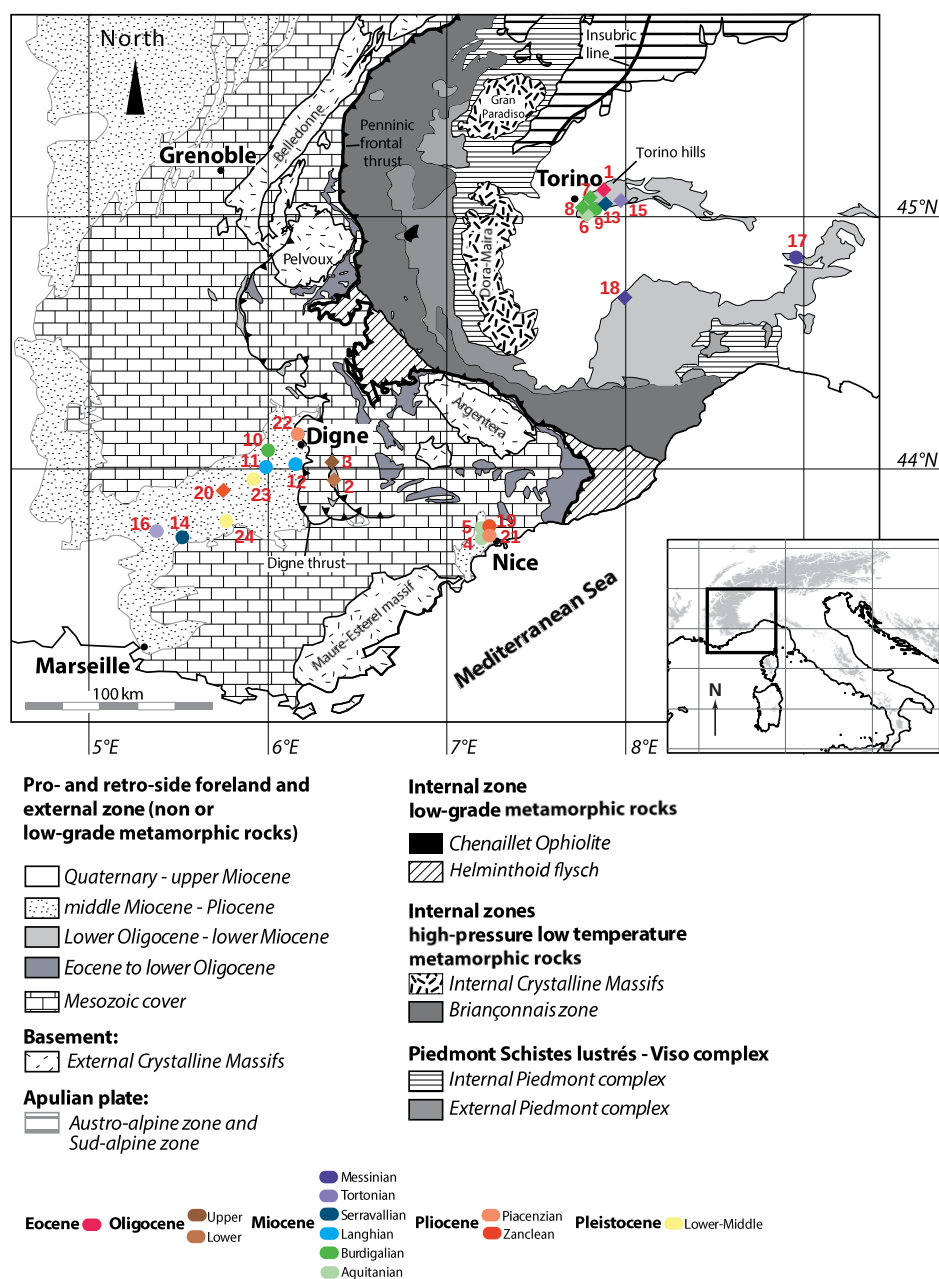


Fig. 20. Carte géologique simplifiée des Alpes de l'Ouest (modifiée d'après Jourdan et al., 2012) et localisation des sites paléogènes et néogènes. Les sites sont numérotés selon leur âge : 1, Gassino Torinese; 2, Saint-Lions; 3, Gambi; 4, Le Gour; 5, Carros; 6, Tetti Civera 1; 7, Tetti Civera 2; 8, Tetti Civera 3; 9, Rio Civera; 10, La Rosée; 11, Les Mées 1 (borehole); 12, Châteauredon; 13, Pavarolo; 14, La Motte d'Aigues; 15, Borelli; 16, Vaugines; 17, Torre Sterpi; 18, Sioneri; 19, Saint-Martin du Var; 20, Villeneuve; 21, Saint-Isidore; 22, Le Rochassas; 23, Les Mées-Périgoite; 24, Oraison-Flour (d'après Fauquette et al., 2015a).

Ces données, bien que peu nombreuses, nous ont permis de reconstituer la végétation, le climat et les paléoaltitudes dans les Alpes du Sud à la fin du Paléogène. Les quantifications du climat à partir de ces données indiquent un climat chaud ($T_a \sim 19^\circ\text{C}$) et humide à basse altitude avec la présence de plantes subtropicales, voire tropicales (mangrove notamment, Fig. 21). Bien sûr, il faut prendre en considération que ces sites étaient 6 à 10° de latitude plus au sud qu'actuellement (Fig. 22 ; Meulenkamp et Sissingh, 2003).

On note également dans ces spectres polliniques la présence de plantes de moyenne altitude (*Cathaya*, *Cedrus*) et même de haute altitude (*Abies*, *Picea*) indiquant des reliefs moyens voire élevés à proximité des sites d'étude dès la fin du Paléogène, 1750 à 1900 m sur la bordure Ouest, 950 à 1800 m sur la bordure Est (Fauquette et al., 2015a).

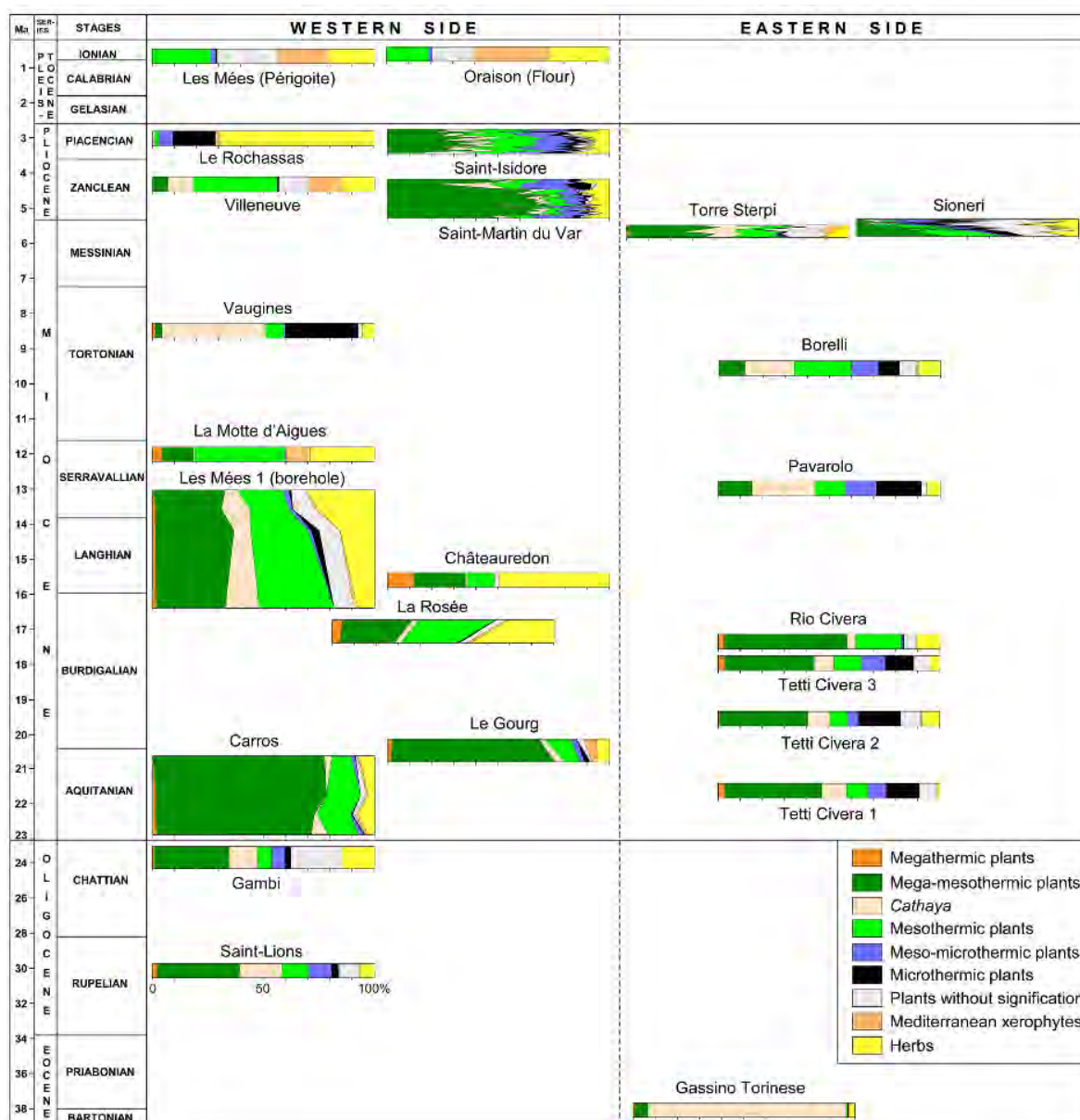


Fig. 21. Diagrammes polliniques synthétiques ayant permis de reconstituer la végétation, le climat et les paléoaltitudes des Alpes depuis la fin de l'Eocène jusqu'au Pléistocène (d'après Fauquette et al., 2015a).

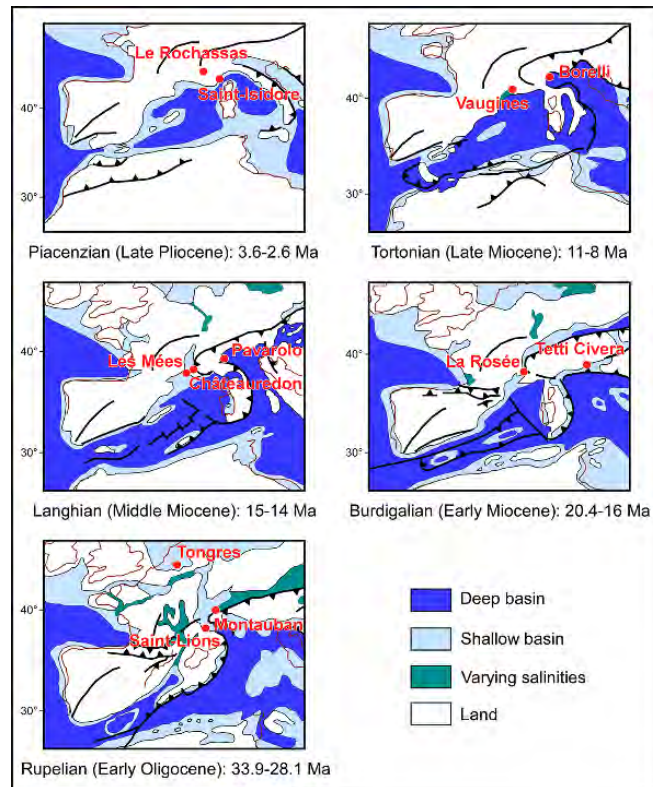


Fig. 22. Cartes paléogéographiques (d'après Meulenkamp et Sissingh, 2003) et localisation des sites des Alpes du Sud-Ouest du Rupélien, Burdigalien, Langhien, Tortonien et Plaisancien (Fauquette et al., 2015a).

3.2. Miocène

Pour cette période, les données polliniques disponibles sont plus nombreuses et nous ont permis de réaliser des reconstitutions des paléoaltitudes pour la Cerdagne, les Alpes du Sud-Ouest et de l'Est et les Apennins.

Cerdagne

Grâce aux données polliniques de deux sites situés en Cerdagne (Fig. 23) Sanavastre/Sampson (Bessedik, 1985) et Can Vilella (Agusti et al., 2006) et aux estimations climatiques qui en découlent, j'ai pu reconstituer l'évolution de la mise en place de ce bassin durant le Miocène supérieur (Suc et Fauquette, 2012).

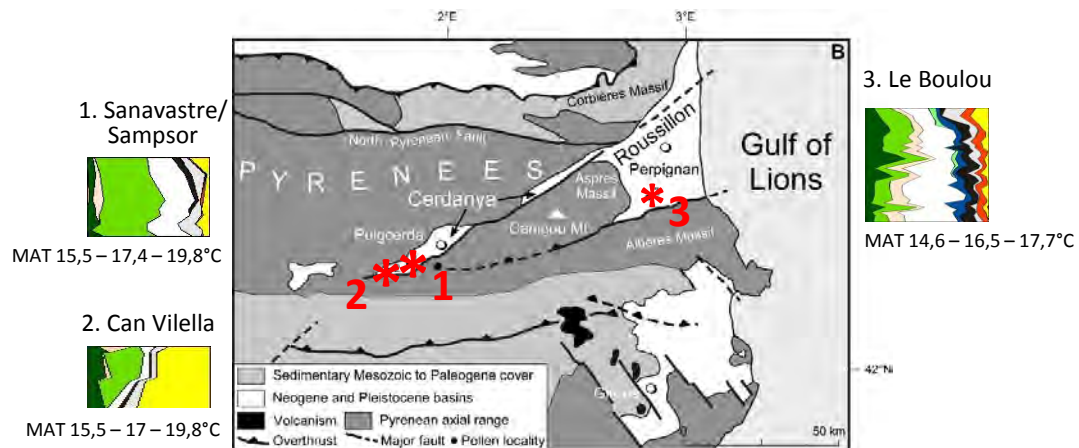


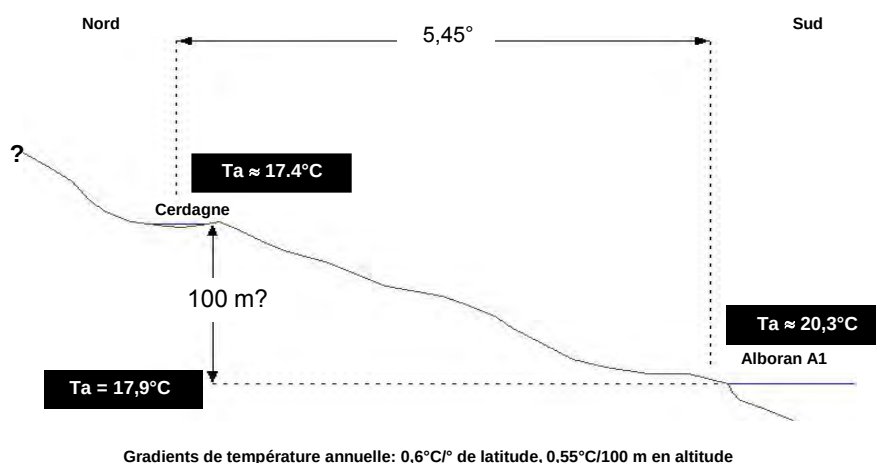
Fig. 23. Géologie régionale, localisation et diagrammes polliniques des séquences de Sanavastre/Sampson (1), Can Vilella (2) et le Boulou (3) (modifié d'après Suc et Fauquette, 2012).

Puisque les sites de Cerdagne sont des sites continentaux, à une altitude *à priori* inconnue, nous avons appliqué dans le cas de ce bassin la deuxième méthode de reconstitution des paléoaltitudes en comparant le climat reconstitué pour la Cerdagne au climat reconstitué sur d'autres sites contemporains au niveau de la mer.

Pour le Tortonien, le site de Sanavastre/Sampsoir a été comparé au site de Alboran A1 (Espagne, Jiménez-Moreno et al., 2010) et pour le Messinien, le site de Can Vilella au site de Capodarso (Sicile, Suc et al., 1995b). Les résultats indiquent que la Cerdagne était à basse altitude durant le Tortonien inférieur (Fig. 24a) puis aux alentours de 600 m d'altitude au Messinien inférieur (Fig. 24b) pour enfin atteindre 1000 m actuellement.

Cela indique un soulèvement constant du Tortonien jusqu'à l'actuel avec un taux de soulèvement d'environ 0.06 à 0.12 mm/an. Par ailleurs, la Cerdagne était, au Miocène, entourée de massifs déjà élevés (Puigmal, Carlit) compte-tenu de la présence non négligeable de grains de pollen de sapin dans les données polliniques alors que le bassin, à basse altitude, était couvert d'une végétation à caractère subtropical.

a. Au Tortonien



b. Au Messinien

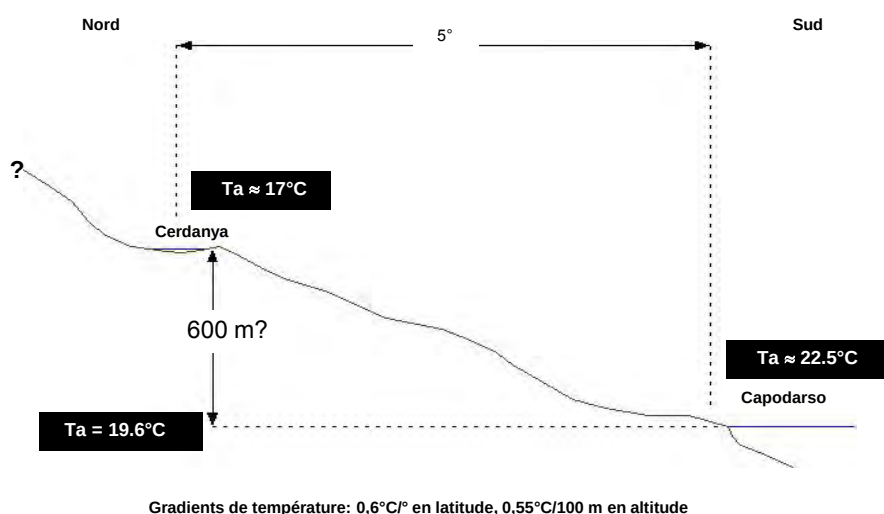


Fig. 24. Comparaison des sites de Sanavastre/Sampsoir (a) et Can Vilella (b) avec des sites contemporains au niveau de la mer.

Des analyses polliniques ont été réalisées sur de nombreux échantillons prélevés sur des coupes réparties dans les Alpes du Sud-Ouest (Figs. 20 et 21 ; Fauquette et al., 2015a) et dans les Alpes de l'Est (Fig. 25 ; Jiménez-Moreno et al., 2008 ; Fauquette et al., sous presse) pour la période du Miocène inférieur au Miocène supérieur (~22 à 8 Ma) afin de restituer les différentes grandes phases de la surrection alpine responsables de la fragmentation des écosystèmes végétaux.

Les reconstitutions de paléoaltitudes en Europe centrale (Paratethys Centrale) mettent en évidence l'absence de reliefs alpins élevés au Miocène inférieur. Toutefois, la présence de *Cathaya* indique des reliefs entre 900 et 1800 m d'altitude. D'un autre côté, la présence du sapin et de l'épicéa à partir Serravallien (14 Ma) indique un soulèvement significatif au Miocène moyen, se poursuivant au Miocène supérieur. Les reliefs des Alpes de l'Est auraient pris de l'importance au Miocène supérieur (Tortonien) et Pliocène inférieur (Fig. 25 ; Jiménez-Moreno et al., 2008) en accord avec l'étude de Kuhlemann et al. (2006).

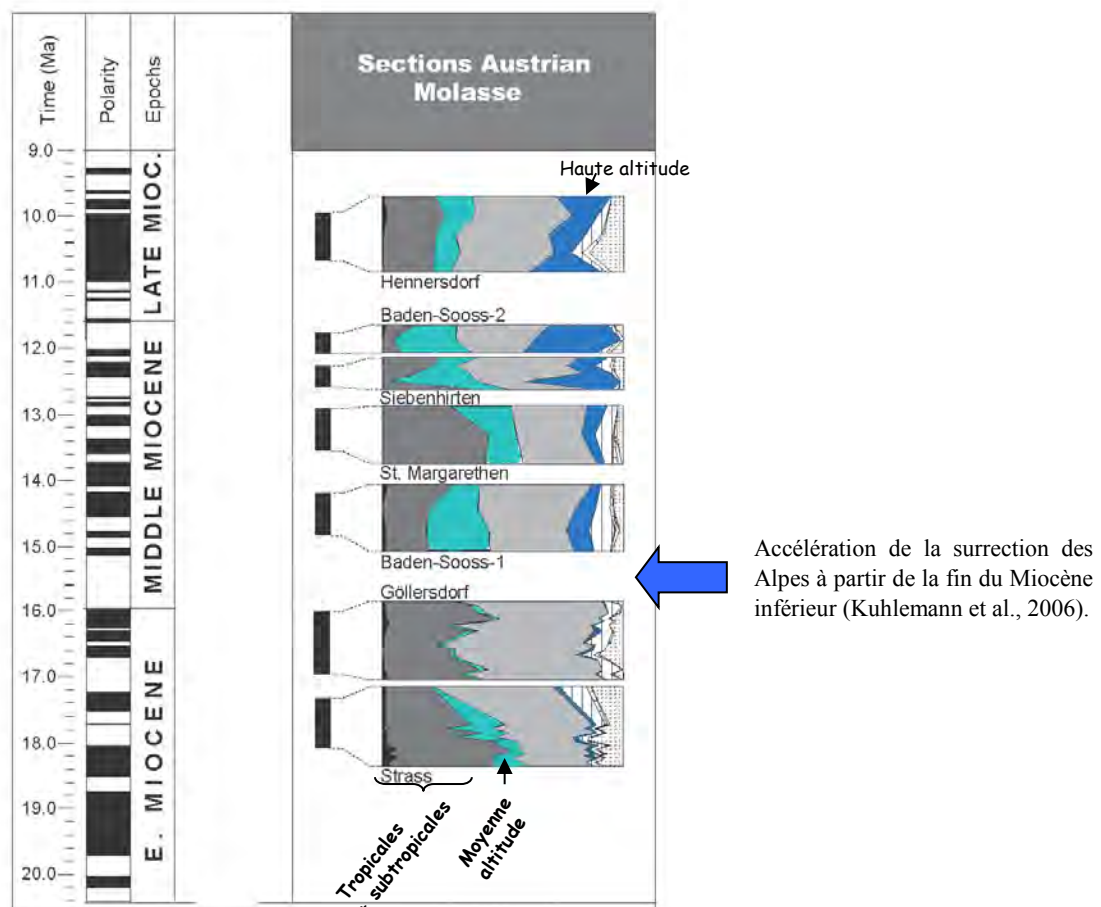


Fig. 25. Diagrammes polliniques synthétiques dans les Alpes de l'Est (d'après Jiménez-Moreno et al., 2008). Mise en évidence de la surrection alpine.

Dans les Alpes du Sud-Ouest, les données polliniques montrent clairement que des reliefs très prononcés existaient dès l'Aquitainien du côté italien du massif mais les données du côté français du massif n'enregistrent pas, au cours du Miocène, de plantes d'altitude de façon significative (Fig. 20). Cette absence peut être due à une distance trop importante entre les montagnes et les sites de dépôt des sédiments (La Motte d'Aigues) ou à l'absence de certains reliefs, comme la nappe de Digne (Châteauredon, Les Mées). Par contre, les forts pourcentages de plantes d'altitude à Vaugines (Fig. 21), au pied du Lubéron (Fig. 20), indiquent que le massif atteignait au moins ~1700 m d'altitude au Tortonien contre 1125 m actuellement, impliquant une forte érosion du massif depuis 10 millions d'années (Fauquette et al., 2015a).

Apennins du centre et du nord

Les Apennins correspondent à une zone orogénique située sur la frontière entre la plaque africaine et la plaque européenne. L'activité volcanique et les séismes actuels caractérisant la péninsule italienne montrent que la tectonique y est toujours active.

J'ai réalisé des reconstitutions paléoenvironnementales (climat et altitude) pour la période allant du Tortonien supérieur au Pliocène inférieur à partir d'analyses polliniques effectuées sur cinq sections sédimentaires situées dans les Apennins du nord et du centre (Fig. 26, Trave, Bertini et Menichetti, 2015 ; Legnagnone, Gennari et al., 2013 ; Cava Li Monti, Bertini, 1994, 2006 ; Maccarone, Bertini, 1994, 2006 ; Stirone, Bertini, 1994, 2001, Fauquette et Bertini, 2003).



Fig. 26. Localisation des coupes des Apennins du Nord et du centre.

Les données polliniques utilisées dans le cadre de cette étude (Fig. 27) ont montré que les changements de végétation au cours du temps reflétaient les variations en altitude des étages de végétation sur les massifs montagneux à proximité. Par ailleurs, les reconstitutions climatiques basées sur ces mêmes données suggèrent qu'à basse altitude les températures moyennes annuelles étaient plus élevées durant la fin du Néogène qu'actuellement (températures annuelles comprises entre 17 et 18°C) comme partout ailleurs en région méditerranéenne (Fauquette et al., 2006, 2007 ; Jiménez-Moreno et al., 2010). Cela implique un déplacement en altitude des étages de végétation pour compenser les hautes températures.

Les résultats obtenus indiquent que les Apennins du nord et du centre étaient soulevés dès le Tortonien, atteignant des altitudes significatives autour de 1350 m, 1500 m à la fin du Miocène dans les Apennins centraux et une altitude minimum autour de 1900 m au Messinien et même 2150 m au Pliocène inférieur dans les Apennins du Nord (Fauquette et al., 2015b).

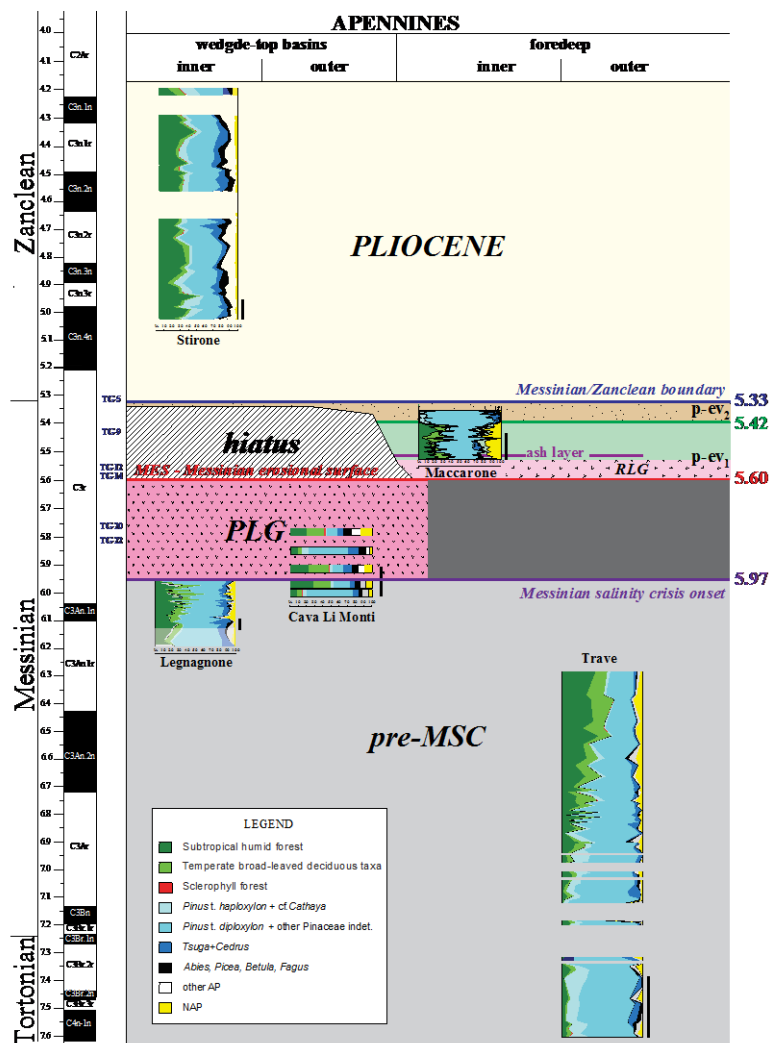


Fig. 27. Données polliniques utilisées pour la reconstitution paléoenvironnementale des Apennins du nord et du centre (Fauquette et al., 2015b).

3.3. Pliocène

Le massif du Canigou, Pyrénées-Orientales

Les données polliniques du Boulou (Pyrénées-Orientales, Fig. 23) nous ont permis de reconstituer la température annuelle sur le littoral de cette région au Pliocène inférieur puis d'en inférer une altitude minimale du Massif du Canigou (Suc et Fauquette, 2012). En effet, l'assemblage pollinique est riche en plantes de moyenne altitude (*Cathaya*, *Cedrus*, *Tsuga*) et de haute altitude (*Abies*, *Picea*) aux cotés de plantes subtropicales et tempérées, ce qui indique une succession de végétation complète, du littoral jusqu'au sommet du Canigou. Au Pliocène inférieur, le climat était chaud et humide à basse altitude, avec des températures annuelles autour de 16.5°C (intervalle de 14.6 à 17.7°C, Fig. 23). Cette température est actuellement enregistrée environ 4° plus au sud que le Boulou. La relation établie par Ozenda (1989) (un déplacement de 1 km vers le nord est équivalent, d'un point de vue bioclimatique à un déplacement de 1 m en altitude) nous indique donc un déplacement des étages de végétation d'environ 440 m en altitude pour compenser les températures élevées de cette époque.

Dans cette région, les forêts à sapins se développent actuellement à partir d'environ 1700 m d'altitude. Considérant le déplacement des étages de végétation de 440 m en altitude lors du Pliocène, cela conduit à une altitude minimale de ~2100 m pour l'étage du sapin. Cela indique donc une altitude minimale de 2100 m pour le massif du Canigou (Suc et Fauquette, 2012).

Alpes du Sud-Ouest

Les données polliniques de Saint-Martin du Var et de Saint-Isidore (Figs. 20 et 21 ; Zheng, 1990) ont été utilisées pour reconstituer le climat (Fauquette et al., 1999a) et les paléoaltitudes des Alpes du Sud au Pliocène basal (Fauquette et al., 1999b). Ces données mettent en évidence des pourcentages relativement élevés en pollen de plantes d'altitude laissant supposer que ces sites étaient proches des montagnes (Mercantour) sur lesquelles l'étage subalpin était bien développé. Compte-tenu de la température annuelle reconstituée ($T_a \sim 16.5^\circ\text{C}$, Fauquette et al., 1999a), les étages de végétation devaient être décalés d'environ 600 m en altitude pour compenser les températures élevées. Actuellement, le sapin se développe, sous forme de forêts à partir d'environ 1400 m d'altitude. Au Pliocène basal, la limite inférieure de la répartition du sapin était donc autour de 2000 m d'altitude. Le massif du Mercantour atteignait donc au moins 2000 m d'altitude à cette époque (Fauquette et al., 1999a).

Les données de Villeneuve (Figs. 20 et 21) contiennent du pollen de plantes de moyenne altitude comme *Cathaya*, indiquant des altitudes autour de 1800 m. Par contre, les données du Rochassas contiennent, elles, des pourcentages significatifs de pollen de plantes d'altitude. Alors que dans les sédiments du même bassin, au Miocène moyen (Châteauredon), on n'avait ni plantes de haute altitude ni plantes de moyenne altitude, cela signifie que la mise en place de la nappe de Digne a eu lieu entre le Miocène moyen et le Pliocène, ce qui confirme les études géologiques sur la nappe de Digne (e.g. Gidon, 1997 ; Fournier et al., 2008).

3.4. Pléistocène inférieur

Le sud des Apennins

Nous avons vu que durant le Pliocène et le Pléistocène, une chaîne de montagne émergeait le long de l'axe actuel des Apennins (Meulenkamp et Sissingh, 2003; Khondkarian et al., 2004). Westaway et Bridgland (2007) parlent d'une "paléo-île" émergeant en Calabre Centrale, entre Cosenza et Crotona (Fig. 28). L'intense soulèvement affectant cette région du Pléistocène moyen à l'Holocène a conduit à l'émersion de sédiments marins déposés à environ 500 m de profondeur (Landini et Menesini, 1978). Ces sédiments sont actuellement à l'affleurement, entre 0 et 400 m au-dessus du niveau de la mer près de Semaforo.

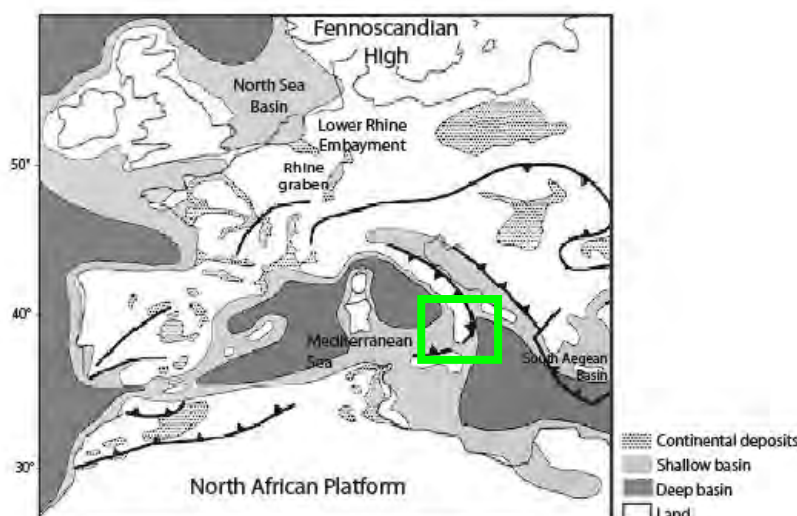


Fig. 28. Carte paléogéographique de la Méditerranée de l'ouest pour la période du Plaisancien/Gelasien (3.4 – 1.8 Ma), modifiée d'après Meulenkamp et Sissingh (2003).

Les changements de végétation passés enregistrés dans les sédiments de Semaforo en Calabre (Combourieu-Nebout, 1993) (Fig. 29) reflètent, ici également, les mouvements des étages de végétation sur la Sila située à une trentaine de kilomètres. Ces changements de végétation, depuis les forêts subtropicales jusqu'à des formations herbacées ouvertes, indiquent des variations de climat correspondant aux interglaciaires chauds et humides et aux glaciaires frais et/ou secs.

A environ 2.4 Ma, Combourieu-Nebout et al. (2000) et Fauquette et Combourieu-Nebout (2013) ont estimé que, à basse altitude, les températures annuelles étaient environ 4°C plus élevées qu'actuellement durant les interglaciaires et équivalentes à l'actuel pendant les glaciaires. Les précipitations annuelles à basse altitude étaient plus élevées qu'actuellement, de l'ordre de 1000 à 1400 mm, durant les interglaciaires et équivalentes à l'actuel, autour de 400 à 500 mm durant les glaciaires.

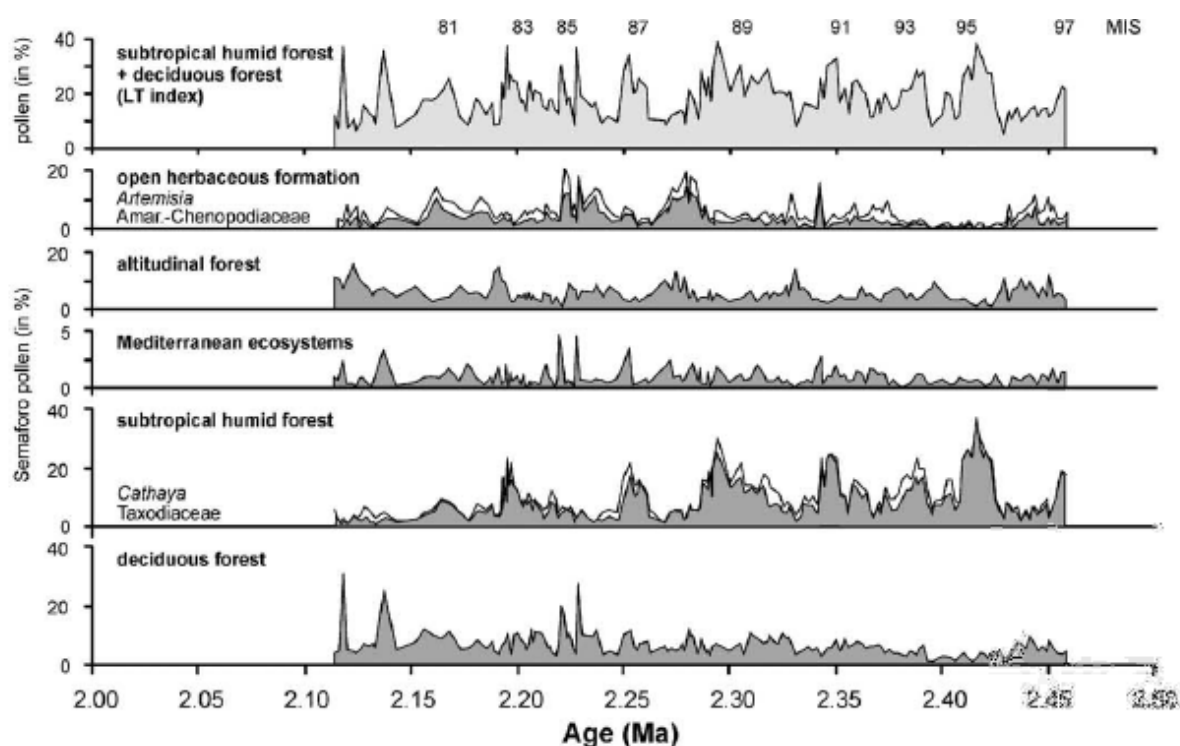


Fig. 29. Diagramme pollinique simplifié de la section Semaforo montrant les fluctuations des principaux groupes de végétation. Les stades isotopiques (MIS) ont été indiqués (d'après Klotz et al., 2006).

A partir des estimations de température annuelle obtenues, nous avons pu estimer que, pour compenser les températures élevées lors d'un interglaciaire, les étages de végétation devaient être décalés d'environ 500 m en altitude. Par contre, ils devaient être en position actuelle durant les glaciaires. Sachant que le sapin (plante de haute altitude/latitude) est actuellement présent à partir d'environ 1600 m d'altitude sur la Sila, nous en avons déduit que la partie sud des Apennins atteignait à cette époque 1600 à 2100 m d'altitude, alors que la région de Crotone était sous ~500 m d'eau. Toutefois, bien que le bassin de Crotone ait été soulevé d'au moins 650 m depuis 2.4 Ma, il n'est pas possible de savoir si la Sila a subi le même soulèvement ou non car le bassin de Crotone est un bassin bordé par des failles.

Par ailleurs, cette étude a également permis de mettre en évidence que, comme le sud des Apennins n'atteignait pas de hautes altitudes, les refuges interglaciaires pour les plantes à affinité boréale telles que le sapin et l'épicéa devaient se situer plus au nord, à plus haute altitude, ou sur l'ubac de la Sila, sous conditions plus fraîches et plus humides.

3.5. Synthèse sur les paléoaltitudes

Nos études ont mis en évidence le potentiel des données polliniques à reconstituer l'histoire des paléoreliefs, d'autant plus si elles sont couplées avec des études sédimentologiques, pétrologiques et thermochronologiques permettant de connaître la provenance des sédiments ainsi que les taux d'exhumation.

A partir de nos résultats nous pouvons établir une carte de synthèse (Fig. 30). Toutefois, pour un massif donné, nous n'avons pas toujours de sédiments suffisamment anciens pour connaître la date de soulèvement : par exemple, nous savons que le massif du Canigou dans les Pyrénées-Orientales atteignait ~2100 m d'altitude au Pliocène inférieur mais nous n'avons pas d'enregistrement du début de sa formation. Pour d'autres, nous avons des données qui permettent d'encadrer la date de soulèvement du massif, c'est le cas pour la nappe de Digne que nous voyons se mettre en place entre 16 et 5 Ma ou encore le Lubéron entre 12 et 8 Ma.

Nous avons mis en évidence que la zone interne des Alpes du Sud-Ouest atteignait une altitude d'au moins 1800 m dès l'Oligocène avec une topographie asymétrique Est/Ouest proche de l'actuel et des reliefs plus hauts et des pentes plus accusées à l'Est qu'à l'Ouest mais que les massifs externes, comme le Mercantour, ont été soulevés plus tard, au cours du Néogène supérieur. Dans les Alpes de l'Est, les données indiquent l'absence de reliefs alpins élevés au Miocène inférieur. Ils auraient pris de l'importance au Miocène supérieur (Tortonien) et au Pliocène inférieur.

Les Apennins du nord et du centre étaient soulevés dès le Tortonien, avec des paléoaltitudes non négligeables (~1350 m dès le Tortonien, 1500 à 1900 m à la fin du Miocène, 2150 m au Pliocène inférieur) permettant l'installation de plantes de type boréal.

Il est à noter que les sites qui étaient marin littoraux pendant le Paléogène ou le Néogène sont de nos jours au-dessus du niveau marin. Le soulèvement s'opère donc tout au long du Néogène et du Quaternaire ancien.

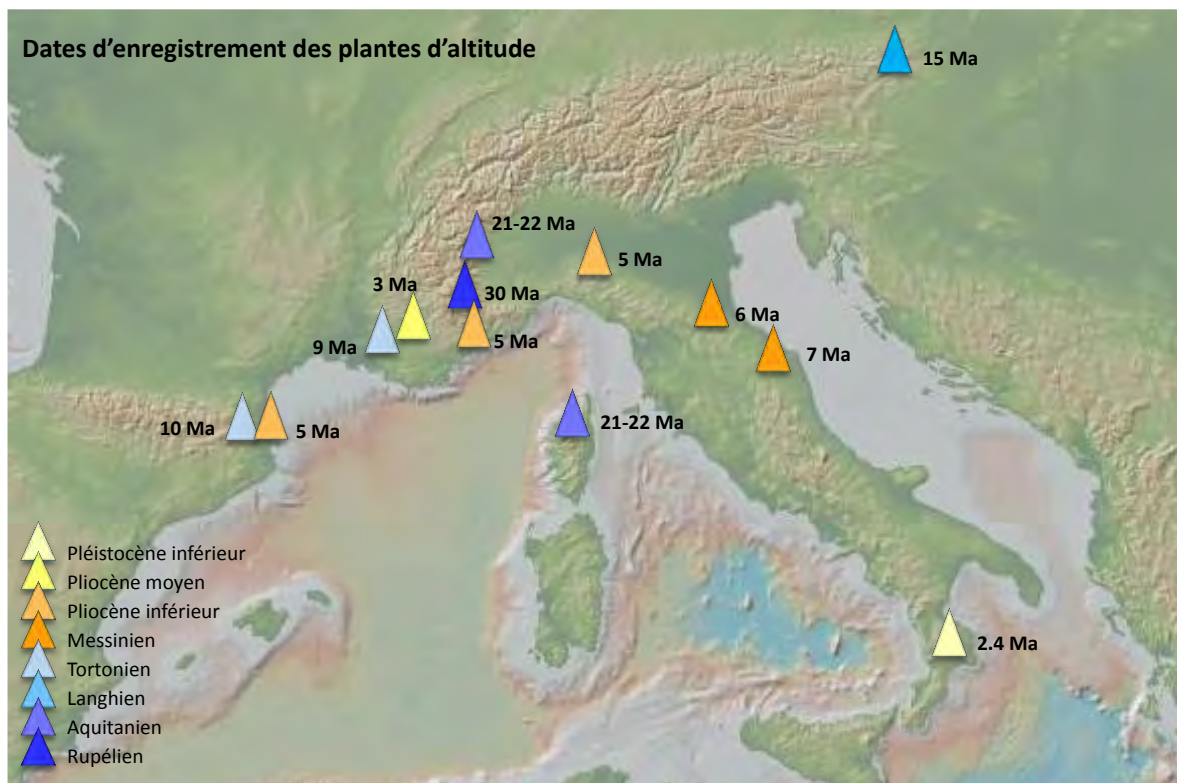


Fig. 30. Dates d'indication de reliefs élevés en Europe de l'Ouest.

4. Conclusion - Géologie, climat, Homme : impacts sur la végétation et la diversité végétale

Tous ces résultats nous ont amené à faire le lien entre la végétation actuelle, géologie, changements climatiques et évolution de la végétation sur une longue période de temps qui a connu de nombreux changements (Fauquette et al., sous presse). Je me suis plus particulièrement intéressée à deux régions-clés en Europe, les Alpes et la région méditerranéenne.

En montagne, en particulier dans les Alpes, les écosystèmes montrent généralement une forte diversité végétale car ils représentent des assemblages complexes influencés par l'altitude, la roche-mère, le sol, les conditions climatiques qui suivent la latitude, la longitude, la pente et l'orientation.

Les Alpes sont un des hotspots de biodiversité les plus importants en Europe avec un grand nombre de plantes endémiques (Ozenda, 2002). La distribution de ces endémiques est essentiellement concentrée dans la région la plus au Sud des Alpes de l'Ouest (Alpes Maritimes, Ligurie) et dans l'extrême Sud des Alpes de l'Est (Noble et Diadema, 2011). La diversité végétale dans les Alpes résulte principalement de la localisation du massif à la transition entre climat tempéré-froid et tempéré-chaud, de la variabilité du climat local due à la complexité de la topographie, mais également résulte de la paléobiogéographie.

Dans les Alpes, l'organisation de la végétation est d'autant plus complexe que le massif est très étendu et qu'il se situe au carrefour de plusieurs provinces floristiques (Ozenda, 2009). De plus, l'arc alpin est principalement orienté Ouest/Est sauf en France où il est orienté Nord/Sud. La partie française est donc caractérisée par d'importantes différences entre le Nord et le Sud, le Sud étant sous influence méditerranéenne, avec un climat plus sec.

La question était de savoir comment la géologie, les changements climatiques et la pression anthropique ont influencé la végétation et la biodiversité dans les Alpes.

La formation de hauts reliefs (~1800 m) dans les Alpes du Sud-Ouest dès 35-40 Ma, au Paléogène supérieur (Fauquette et al., 2015b), dans une région où le climat était tempéré-chaud voire subtropical, a permis le développement d'environnements de type boréaux à haute altitude. Des arbres méso-microthermes (*Cedrus*, *Cathaya*) et microthermes (*Abies*, *Picea*) ont ainsi pu s'y installer.

La formation des écosystèmes alpins s'est faite à partir de 2 sources de plantes, une source autochtone et une source allochtone. La source autochtone est composée de plantes subtropicales à tropicales qui se sont progressivement éteintes au fil de la compétition et des glaciations du Pléistocène. Seuls quelques taxons ont survécu dans les Alpes de l'Ouest comme *Juniperus thurifera* et *Berardia subacaulis* (Ozenda, 2009). La source allochtone est composée des plantes ayant migré, au fil des périodes froides, depuis les régions arctiques et/ou régions montagneuses asiatiques (Ozenda, 2009, Kadereit et al., 2008). Toutefois, la flore alpine montre plus d'affinités avec les flores du sud (bassin méditerranéen, Asie centrale et orientale) qu'avec les flores nordiques (Scandinavie, Amérique du Nord, Comes et Kadereit, 2003) grâce à des connections plus ou moins continues avec les systèmes montagneux asiatiques (Altaï, Tibet, Himalaya).

Les glaciations du Pléistocène ont joué un rôle majeur dans les changements de végétation en éliminant progressivement les plantes les plus thermophiles, en contraignant les plantes

tempérées dans des zones refuges conduisant à la disjonction de leurs aires de répartition et en amplifiant les échanges avec les régions arctiques et/ou montagneuses asiatiques. A l'opposé, durant les interglaciaires, la réinstallation des plantes tempérées pousse les plantes microthermes vers des régions plus froides, en altitude ou à plus haute latitude.

Le dernier maximum glaciaire (24–17 ka) signe le *point zéro* de la végétation dans les Alpes avec une régression maximale des plantes tempérées au bénéfice des plantes de type boréal.

Le retour aux conditions plus douces de la période post-glaciaire permettra l'installation progressive de la végétation alpine telle qu'on la connaît aujourd'hui. Toutefois l'activité anthropique (exploitation forestière, pâturage) a eu un fort impact sur la végétation d'altitude dans les Alpes depuis le début du Néolithique (~5.5 ka).

En ce qui concerne la région Méditerranéenne, de par sa situation entre l'Eurasie et l'Afrique, elle a été peuplée d'une végétation en provenance de ces deux régions. Les échanges entre ces deux domaines ont été facilités par l'existence de microplaques depuis le Crétacé inférieur (Biju-Duval et Montadert, 1977). Sa flore se compose donc à la fois d'éléments d'origine tropicale, septentrionale et d'éléments autochtones. Par ailleurs, les reliefs élevés permettent une pénétration des éléments boréaux en altitude dans cette région tempérée.

De nombreuses plantes tropicales sont encore présentes en région Méditerranéenne au début du Néogène (*Avicennia*, *Acacia*, Bombacaceae par exemple, Bessedik et al., 1984 ; Bachiri Taoufiq, 2000 ; Jiménez-Moreno, 2005). Des éléments relictuels, souvent d'origine tertiaire, comme notamment *Laurus azorica*, *Argania spinosa*, *Acacia gummifera*, *Cedrus atlantica*, *Tetraclinis articulata* (Thuya de Berbérie) et, trouvé très récemment, le Dragonnier (*Dracaena draco* subspecies *ajgal*), sont encore présents au Maroc (Quézel et Médail, 2003) ou encore *Zelkova sicula* en Sicile (Di Pasquale et al., 1992), *Zelkova abelicea* en Crète (Barbero et Quézel, 1980 ; Quézel et Médail, 2003) et *Phoenix theophrasti* en Crète et Turquie (Quézel et Médail, 2003).

Cependant, au fil du refroidissement global au cours du Néogène, nombre de ces plantes tropicales disparaissent au profit d'éléments subtropicaux et tempérés. Plus particulièrement, le refroidissement progressif du Quaternaire depuis 2.6 millions d'années, au cours duquel se mettent en place les cycles glaciaire-interglaciaire aux extrêmes de plus en plus marqués (Klotz et al., 2006), semble expliquer l'appauvrissement de la flore (Suc et al., 1995b). La mise en place des forts contrastes saisonniers actuels pourrait également l'expliquer.

Finalement, le Tardiglaciaire a entraîné le déclin des essences arborées dans la majeure partie de la Méditerranée mais une expansion des ligneux dans les régions arides du Proche-Orient (Bottema, 1995). A la fin de la dernière phase glaciaire, la recolonisation des milieux s'est faite à partir de refuges méridionaux (péninsule ibérique, Italie, Balkans, Afrique du Nord, Turquie). Par contre, la mer Méditerranée, le Sahara et les chaînes de montagnes des Pyrénées et des Alpes ont joué un rôle de barrière et ont conduit au morcellement des habitats floristiques en empêchant ou en freinant l'avancée des végétaux dans le sens Nord-Sud. En particulier, le cèdre a été évincé de la marge Nord-occidentale de la Méditerranée entre 500 et 700 000 ans sous l'intensification du froid et de la sécheresse au Pléistocène (Pons, 1998) et ne s'est jamais réinstallé ensuite alors qu'il s'est maintenu et même bien développé au sud de la Méditerranée, dans des zones montagneuses humides, où il a trouvé refuge sous un climat moins froid.

En région Sud-Méditerranéenne, la végétation de type xérique ouvert qui existe depuis le Néogène avec une flore dominée par les herbacées et renfermant des éléments subdésertiques comme *Nitraria*, *Neurada*, *Lygeum* et *Calligonum* puis des éléments steppiques comme *Artemisia*, indique que les steppes Sud-méditerranéennes sont sans conteste d'origine climatique

même si l'activité anthropique en Afrique du Nord a fortement contribué à leur maintien voire leur expansion pendant les derniers millénaires.

Par le jeu de la construction des reliefs et des modifications climatiques, la végétation de l'Europe de l'Ouest s'est donc progressivement mise en place telle que nous la connaissons aujourd'hui. Ou plutôt telle qu'elle était avant l'emprise humaine

Travaux en cours et en perspectives

Mes objectifs pour les années à venir sont dans la continuité de mes travaux jusqu'à présent réalisés ou en cours de réalisation.

Forte de mon expérience acquise sur le Cénozoïque européen, il me semble maintenant évident d'étendre mes études dans l'espace et dans le temps :

- dans l'espace parce que de nombreuses régions sont actuellement moins bien connues au niveau paléoenvironnemental (végétation, climat, topographie, paléogéographie) alors qu'il est nécessaire de connaître leur évolution dans une optique paléobiogéographique,
- dans le temps parce qu'il faut remonter bien au-delà de l'Oligocène pour connaître la paléogéographie et les paléoclimats pour affiner les modélisations climatiques et pour comprendre les origines des flores et de la diversité végétale. En particulier, nous savons que l'Éocène inférieur (56-48 Ma) représente une période remarquablement chaude présentant de très faibles gradients thermiques entre l'équateur et les pôles (Huber et Caballero, 2011). Les modèles numériques, dans les limites imposées par les teneurs en CO₂ estimées pour cette période (Hoareau et al., 2015 ; Jagniecki et al., 2015), sous-estiment systématiquement les températures (Sagoo et al., 2013). Une meilleure reconstitution des conditions paléoenvironnementales à cette période est ainsi primordiale pour mieux étalonner les modèles des climats passés et futurs.

Il faudra par ailleurs que je continue à améliorer la base de données des amplitudes climatiques supportées par les plantes, notamment en travaillant en collaboration avec le Prof. Zhuo Zheng de l'Université de Canton (Chine) afin d'intégrer des plantes que l'on ne trouve actuellement qu'en Chine. En effet, son équipe dispose d'une conséquente base de données de spectres polliniques actuels (2858 sites) répartis en Chine et au Japon dans différents biomes (East Asian Pollen Database, Zheng et al., 2014). Cela me permettra de définir la distribution des pourcentages polliniques de taxons représentés dans les spectres actuels asiatiques en fonction des valeurs climatiques correspondantes, en particulier des taxons tropicaux, que nous voyons apparaître dans les spectres fossiles au fur et à mesure des nouvelles périodes ou des nouvelles régions étudiées.

1 - Etendre mes recherches dans l'espace

1.1. Marge marocaine de la mer d'Alboran

Dans le cadre projet *MEDYNA* (programme FP7-PEOPLE-IRSES, responsables : C. Garrido, Grenade et J.-L. Bodinier, Géosciences Montpellier) et faisant suite au projet financé par le PHC Volubilis et par le GDR Marges en 2011 et 2012 (responsable : P. Münch, Géosciences Montpellier), je continue à étudier l'évolution de la végétation au cours du Néogène dans le Nord du Maroc car, s'il est maintenant bien admis que les steppes marocaines sont d'origine climatique (l'homme ne venant que renforcer cet aspect steppique) et très anciennes, datant au moins du Miocène (Feddi, Fauquette & Suc, 2011 ; Amami et al., 2013), la présence et le développement de certaines plantes comme le cèdre soulèvent encore des questions. Depuis quand le cèdre est-il présent au Maroc et à partir de quelle date s'est-il abondamment développé ? Les données polliniques peuvent permettre de répondre à ces questions cruciales, notamment pour l'avenir du cèdre dans cette région sous la contrainte du réchauffement climatique à venir.

Un des objectifs de ces projets est également d'estimer le timing et la vitesse d'exhumation de la marge Sud-Alboran au cours des 15 derniers millions d'années. La marge marocaine de la Mer d'Alboran est limitée au Sud par la chaîne du Rif qui s'élève rapidement à plus de 2200 m et au Nord par les bassins Ouest- et Sud-Alboran qui s'enfoncent jusqu'à 2200 m et 1000 m respectivement. La présence de ces reliefs traduit des phénomènes tectoniques récents, pour la plupart d'âge Néogène à actuel. Le nord du Maroc est caractérisé par des tremblements de terre fréquents, parfois de forte amplitude (*e.g.*, à Al Hoceima en 2004, avec une magnitude de 6.3), qui induisent des mouvements verticaux importants. Par exemple, dans la région de Oued Laou, la présence de dépôts sédimentaires pliocènes surélevés jusqu'à des altitudes de 500 m montre clairement que cette région a subi des mouvements verticaux importants pendant les 5 derniers millions d'années.

L'étude de ces mouvements verticaux et de leur timing nécessite de prendre en compte le couplage entre la tectonique, comme moteur de la création des reliefs, et les processus de surface responsables de la destruction des reliefs.

Les mouvements verticaux seront estimés en croisant trois méthodes : les reconstitutions paléoenvironnementales des bassins miocènes et pliocènes, les données thermochronologiques basse température (datations U-Th/He) et la reconstitution des paléoaltitudes à partir des données polliniques dans ces mêmes bassins. Grâce à une calibration fine du timing des événements (échelle de 100 à 400 kyrs) par l'utilisation conjointe des nannofossiles calcaires, des foraminifères planctoniques et de la géochronologie absolue (Ar^{40}/Ar^{39} sur niveaux de cendres et U/Th sur organismes aragonitiques), il sera possible de suivre l'évolution des reliefs en fonction du temps entre -10 Ma environ et l'Actuel, et de reconstituer l'histoire et l'amplitude des mouvements verticaux.

Dans cette optique, des échantillons sédimentaires provenant de plusieurs coupes dans le bassin de Boudinar (Rif, Maroc) ont été prélevés afin de réaliser une étude palynologique sur cette zone de la marge sud-Alboran où la biostratigraphie, des datations $^{40}Ar/^{39}Ar$ et des analyses sédimentologiques ont déjà été faites (Achalhi et al., 2016). Les sédiments de la coupe d'Irhachâmene (Fig. 31) ont d'ores et déjà livré des données polliniques couvrant le Tortonien supérieur et le début du Messinien. L'interprétation conjointe de toutes les proxies analysées nous ont permis d'établir un scénario concernant les connections océan/Méditerranée au cours du Miocène.

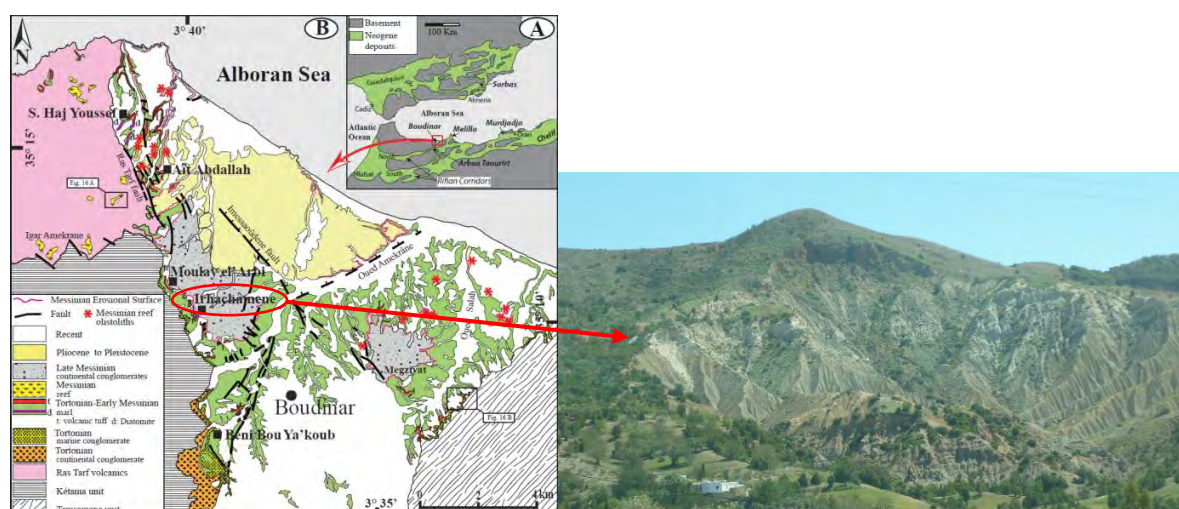


Fig. 31. Carte géologique simplifiée du bassin de Boudinar et photo de la coupe d'Irhachâmene.

A la fin du Tortonien, les données polliniques, avec peu de pollens de pin indiquent la proximité du point de sédimentation par rapport au littoral (Fig. 32). Par ailleurs, la richesse en plantes herbacées et halophytes (supportant des conditions un peu salées), indiquent une végétation ouverte sur le littoral de cette région. Les forêts devaient être rares et plutôt disposées sur les reliefs de l'arrière-pays. Par contre, l'absence d'arbres de haute altitude, nous permettent d'avancer 3 hypothèses : 1) Boudinar était un petit bassin versant sans hautes montagnes, 2) les montagnes étaient trop éloignées du point de sédimentation, 3) le Rif n'était pas encore complètement soulevé et donc trop bas pour autoriser le développement des arbres d'altitude comme le sapin. Le climat, estimé d'après ces données, était chaud et aride, avec des précipitations inférieures à 500 mm/an.

Toutes les proxies utilisées dans cette étude suggèrent qu'à la fin du Tortonien, le bassin de Boudinar était un golfe peu profond entouré de reliefs peu élevés (Achalhi et al., 2016).

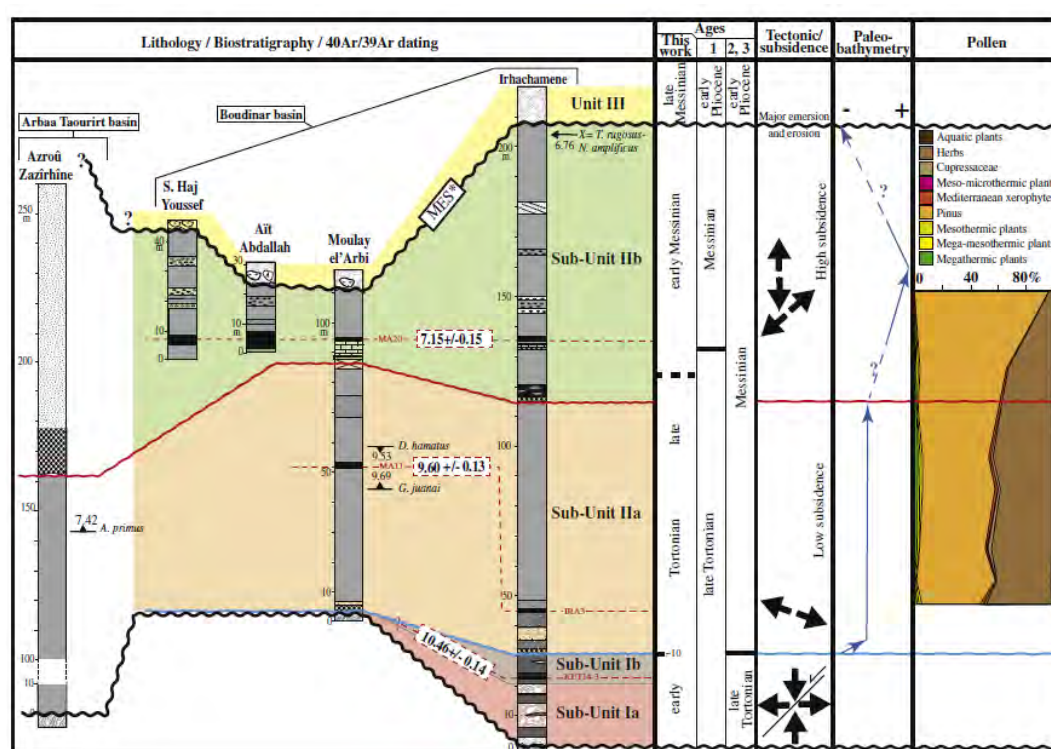


Fig. 32. Synthèse des données biostratigraphiques, radiométriques et polliniques pour le bassin de Boudinar. Corrélations entre les différentes coupes (d'après Achalhi et al., 2016).

A la transition Tortonio-Messinienne, les données polliniques (Fig. 32) montrent une augmentation significative des pollens de pin et une diminution des pollens de plantes halophytes indiquant un éloignement du point de sédimentation par rapport au littoral, en accord avec les autres données qui indiquent un approfondissement du bassin. Les données polliniques n'indiquent aucun changement climatique depuis le Tortonien. Les variations des pourcentages polliniques sont uniquement contrôlées par les variations du niveau marin. Au début du Messinien, le bassin de Boudinar était un bassin ouvert et profond et le trait de côte était relativement éloigné.

Dans ce travail, toutes les données, y compris polliniques, sont en accord et indiquent que la sédimentation marine commence à ~10 Ma (Tortonien inférieur) dans le bassin de Boudinar et

persiste jusqu'à ~6 Ma (fin du Messinien inférieur). Achalhi et al. (2016) mettent en évidence les modifications des connections Méditerranée-Atlantique par le corridor nord-Rifain au Miocène supérieur, modifications qui ont très certainement eu un impact sur la végétation (migration de végétaux entre Sud de l'Europe et Afrique du Nord). A la fin du Tortonien, le corridor Nord-Rifain s'ouvre et devient le passage majeur des eaux atlantiques vers la Méditerranée après 7.2 Ma. Puis, au Messinien supérieur, les connections Atlantique/Méditerranée par le corridor Nord-Rifain deviennent de plus en plus restreintes et finissent par se fermer à ~6.1 Ma.

➤ Ces premiers résultats très prometteurs nous incitent à poursuivre l'étude de cette zone du Maroc afin de reconstituer les paléoreliefs dans cette région. En effet, peu d'études existent et il est difficile d'établir les dates de mise en place du massif du Rif et les paléoaltitudes. Les résultats que nous avons obtenus à partir de la coupe d'Irhachâmene laissent penser que qu'il n'y avait pas, au Miocène supérieur, de reliefs élevés dans l'arrière-pays de Boudinar ou du moins que les reliefs étaient trop éloignés pour que l'on puisse enregistrer le pollen de plantes d'altitude (cèdre, sapin) dans les sédiments de ce bassin, ce qui confirme d'autres données palynologiques couvrant le Tortonien et le Messinien inférieur dans le corridor rifain (Bachiri-Taoufiq and Barhoun, 2001; Bachiri-Taoufiq et al., 2001, 2008).

Afin de répondre à la question de la formation du Rif, je travaillerai sur des sédiments prélevés sur la coupe de Bahr Sidi Driss, également dans le bassin de Boudinar (Fig. 33). Ces sédiments, dont nous savons d'ores et déjà qu'ils sont d'âge Pliocène inférieur à Pliocène moyen (Achalhi, Cornée et Münch, comm. pers.), nous permettront de connaître l'évolution de la végétation dans cette région (en particulier, voit-on arriver le cèdre dans le Rif ?) entre le Miocène supérieur et le Pliocène inférieur puis d'en inférer des estimations climatiques et des reconstitutions de paléoaltitudes.

Enfin, une macroflore découverte dans ce même bassin a été échantillonnée et sera étudiée par une étudiante de Master 2 en 2017 (co-encadrement avec S. Muller, ISEM). Cette macroflore, la seule connue au Maroc, déposée à ~5 Ma, permettra de compléter l'étude paléofloristique du Pliocène de Boudinar et de travailler sur les aspects paléobiogéographiques.

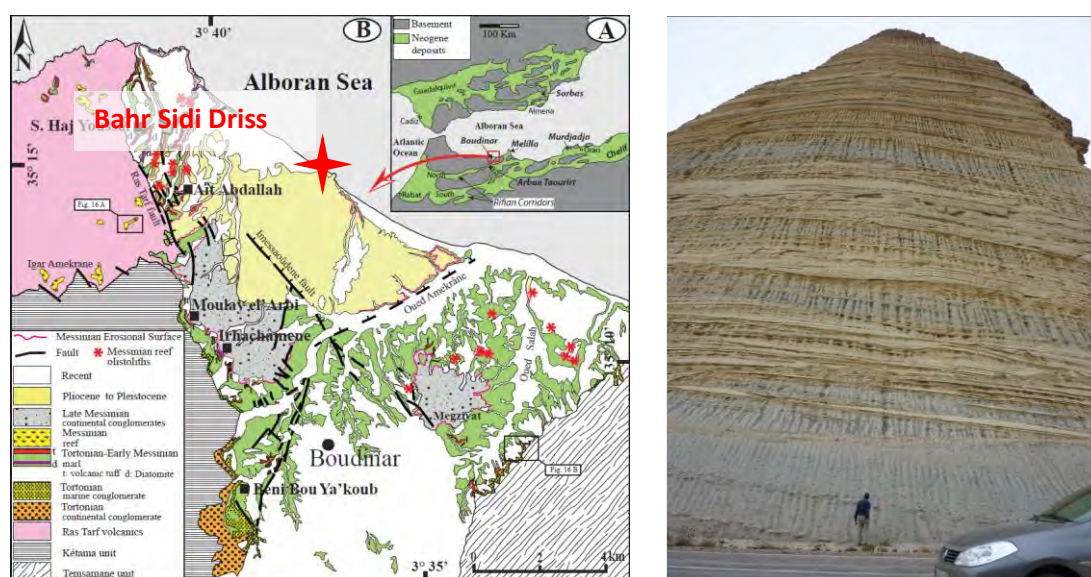


Fig. 33. Localisation de la coupe de Bahr Sidi Driss sur la carte géologique simplifiée du bassin de Boudinar (Achalali et al., 2016) et photo de la coupe.

1.2. Reconstitutions paléoenvironnementales des Andes Centrales au Néogène

La question ici est de savoir comment et quand la flore et la végétation se sont mises en place dans le contexte des mouvements verticaux des Andes centrales, de la paléogéographie et des changements du climat qui ont affecté la région au cours du Néogène.

Les paléoenvironnements de l'Amazonie occidentale, datant du Néogène (23 à 2.5 Ma), restent peu connus, et sont l'objet de nombreux débats entre géologues, paléontologues et palynologues. Les études palynologiques disponibles pour cette région concernent majoritairement le Plio-Quaternaire andin (Hooghiemstra et Ran, 1994), sans remonter au Miocène qui correspond pourtant à la période-clé, ou bien concernent la zone colombienne bien plus au nord (Wijninga, 1996), ou encore qui n'ont pas donné lieu à des valeurs quantifiées (Hoorn et al., 2010).

Pourtant, l'histoire du massif des Andes Centrales est capitale d'un point de vue végétation (mélange des flores septentrionales et tropicales, origine des végétations tropicales arides, origine des associations arborées composées de Bombacaceae/Mimosaceae/Cactaceae présentes dans les milieux semi-arides de l'ensemble de la bande tropicale sud-américaine, depuis le Nordeste brésilien jusqu'au Chaco paraguayen en passant par la vallée sèche inter-andine) mais aussi climatique (refroidissement global, courant de Humboldt, El Nino) et tectonique (dates de soulèvement des Andes, paléoaltitudes).

De plus, la plupart des études palynologiques préexistantes pour le Miocène en Amérique du Sud sont basées sur la détermination morphographique des grains de pollen (*e.g.* Hoorn, 1993, 1994, 2006; Jaramillo et al., 2010; Latrubesse et al., 2010). Or, depuis les années 60, un important changement est intervenu dans la philosophie des palynologues étudiant le néogène européen puisqu'ils utilisent l'approche quaternariste qui repose sur l'identification botanique des grains de pollen (Suc et al., 2004). La paléoécologie se basant sur l'écologie des espèces actuelles pour reconstituer un paléoenvironnement (Hoorn, 1994; Jaramillo et al., 2010; Latrubesse et al., 2010) il est nécessaire d'utiliser l'approche quaternariste.

Dans ce cadre, des échantillons de sédiments néogènes déposés dans la mer miocène Pebas au Pérou (prélevés par P.O. Antoine, ISEM) dans la région d'Iquitos et de Tarapoto (Fig. 34) ont d'ores et déjà été analysés par A. Feussom Tcheumeleu, étudiant que j'ai co-encadré avec M.P. Ledru en M1 et M2 afin d'identifier les changements de végétation au cours du Miocène dans cette région. Il s'est tout d'abord attaché à cataloguer les pollens fossiles en leur donnant une identité taxonomique actuelle puis a regroupé ces taxons en groupes écologiques d'après la littérature afin de pouvoir faire par la suite une reconstitution des paléoenvironnements.

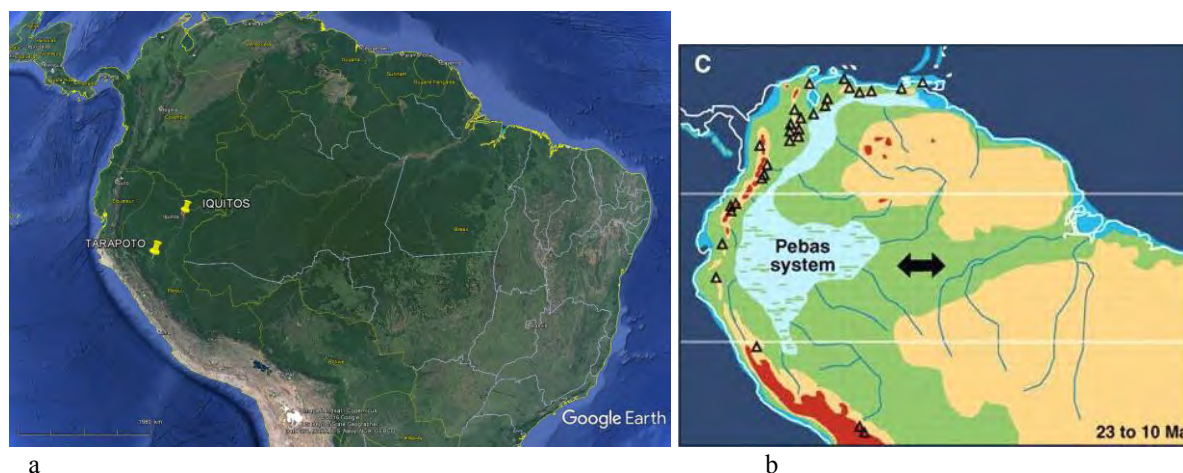


Fig. 34. a) Localisation des affleurements miocènes d'Iquitos et de Tarapoto au Pérou et b) mer Pebas au Miocène (d'après Hoorn et al., 2010).

Les premiers résultats des analyses polliniques de la région d'Iquitos et Tarapoto au Pérou (Fig. 35) ont permis de préciser sur la base de l'écologie des taxons, qu'entre le Miocène moyen et le début Pliocène (14-4 Ma), la végétation péruvienne était dominée par des Angiospermes, dans une mosaïque des paysages partagée entre forêts marécageuses, marais, forêts alluviales et ripisylves. Entre 7 et 4 Ma, le bassin de l'Amazonie se met en place peu à peu, mais à Tarapoto la végétation du type Pebas se maintient même si la ripisylve se développe fortement, ce qui confirme que la mise en place du bassin Amazonien tel qu'on le connaît actuellement s'est faite progressivement dans le temps et d'une localité à l'autre. Cependant, la période exacte à laquelle cette transition a eu lieu reste à déterminer. Enfin, aucun des taxons identifiés n'étant caractéristique d'un environnement marin, il semblerait qu'il n'y aurait pas eu d'incursion marine à Iquitos et à Tarapoto entre le Miocène moyen et le début Pliocène (Feussom Tcheumeleu, 2016).

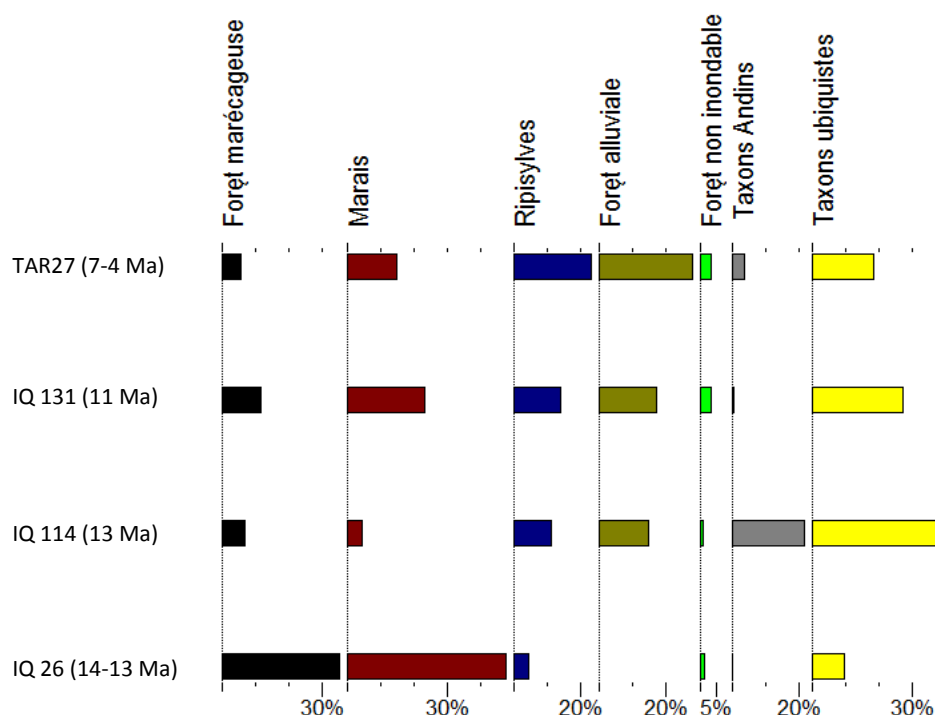


Fig. 35. Diagramme pollinique simplifié des affleurements à Iquitos (IQ131, IQ114, IQ26) et Tarapoto (TAR27) (modifié d'après Feussom Tcheumeleu, 2016).

➡ Cette étude des environnements mio-pliocènes amazoniens va être poursuivie sur des échantillons qui vont être prélevés sur des terrasses fluviales le long du fleuve Maroni en Guyane dans le cadre du projet *Source* (resp. P.O. Antoine) financé par le *Labex CEBA* dont certains membres de l'ISEM font partie. Cela nous permettra, dans une région où aucune donnée palynologique n'existe, de réaliser des études paléoenvironnementales couplées avec les fossiles de vertébrés collectés dans les mêmes niveaux. Une première étude palynologique sera réalisée par un étudiant de Master 2 qui deviendra alors le seul spécialiste de la végétation Néogène de Guyane.

➡ Parallèlement, dans le cadre d'un projet financé par *ECOS-Sud* et par le *National Geographic* en collaboration avec l'Argentine (resp. P.O. Antoine, ISEM), une étude pluridisciplinaire est actuellement menée sur des sites de l'Altiplano. L'Altiplano est un bassin endoréique qui se remplit de matériel détritique depuis le début de la surrection des Andes. Ce

bassin recèle un registre de vertébrés fossiles particulièrement riche pour la période considérée (Miocène moyen à supérieur). A Pomata Ayte (Bolivie, 3800 m d'altitude, Fig. 36 et 37), une coupe de près de 1000 m d'épaisseur a été levée mettant en évidence 8 niveaux fossilifères couvrant le Miocène moyen, le Miocène supérieur, le Pliocène et le Pléistocène. Cette série est entrecoupée de 17 niveaux de tufs, actuellement en cours de datation (P. Münch, Geosciences-Montpellier), qui permettront d'avoir des datations absolues et de caler chronologiquement tous les échantillons prélevés.



Fig. 36. Localisation du site de Pomata Ayte plus au Sud que les sites de Tarapoto et Iquitos.



Fig. 37. Panorama de la série de Pomata Ayte, Altiplano bolivien (photo P.O. Antoine).

Les échantillons prélevés pour la palynologie sont en cours d'étude (M. Pramparo, CONICET-Mendoza, Argentine). Ces échantillons nous apporteront des informations précieuses quant à l'évolution de la végétation sur l'Altiplano au cours du Néogène. Les données nous permettront ensuite d'estimer le paléoclimat et les paléoaltitudes à différents moments clé du Néogène et donc de mieux contraindre la date de surrection de l'Altiplano qui semblerait débuter il y a environ 30 Ma. Sur la base d'une macroflore datant de ~10.66 Ma, Gregory-Wodzicki (2002) estime, en accord avec l'étude de Hoke et Garzzone (2008) basée sur une compilation des paléosurfaces, que l'Altiplano atteignait une paléoaltitude d'un peu plus de 1000 m. Certains auteurs indiquent, sur la base de reconstitution des précipitations à partir d'analyses isotopiques, que des changements importants dans les précipitations ont eu lieu autour de 9-8 Ma, suggérant une configuration proche de l'actuel pour conduire au patron moderne des précipitations en Amérique du Sud (Mulch et al., 2010). Si tel est le cas, nous pourrions voir au travers des données polliniques que la végétation de ce bassin passe d'une végétation de type tropical, chaud et humide, à une végétation de type subtropical-sec puis à une végétation de type steppique voire sub-désertique à la fin du Néogène.

2. Etendre mes recherches dans le temps

Paléoaltitudes des Pyrénées depuis la fin du Paléocène (~58 Ma)

Dans le cadre du projet ANR *PYRAMID* porté par Mary Ford (CRPG, Nancy), des études multidisciplinaires ont été engagées. Elles concernent les interactions entre la déformation, les processus de surface, l'influence du climat durant la formation de la chaîne pyrénéenne et de leurs influences sur les flux de matière.

La tâche 3 de ce projet à laquelle je participe (resp. F. Mouthereau, GET Toulouse), concerne notamment la reconstitution des paléoaltitudes des Pyrénées. Nous savons que la migration vers le Nord des plaques africaine et ibérique a conduit à la formation de la chaîne des Pyrénées sur une période allant du Santonien supérieur (Crétacé supérieur) au Miocène inférieur (Néogène inférieur), soit sur environ 60 millions d'années. Actuellement, les Pyrénées forment une imposante barrière orographique détournant les vents d'ouest chargés d'humidité ce qui conduit à un gradient de précipitation différent entre les flancs nord et sud de cette barrière. Un des buts de notre étude est, en plus de mieux cerner le timing de la surrection des Pyrénées, de déterminer la date d'initiation de cette dissymétrie dans les précipitations.

Mes travaux ont permis dans un premier temps de reconstituer les paléoclimats et les paléoreliefs au Néogène (Miocène et Pliocène) en Cerdagne et dans les Pyrénées-Orientales (Suc et Fauquette, 2012). Si dans le premier cas (Cerdagne), on voit bien le soulèvement continu du bassin entre le Miocène et l'actuel, on ne voit pas pour le deuxième cas (Canigou) le début du soulèvement du massif puisqu'il atteignait déjà 2100 m d'altitude au Pliocène inférieur (Suc et Fauquette, 2012).

➡ Il faut donc compléter ces études afin d'avoir un suivi sur un temps plus long qui nous permettrait de voir la mise en place de la chaîne pyrénéenne.

Pour répondre à attente, je travaillerai à partir de données polliniques réalisées ou en cours de réalisation sur des sédiments cénozoïques du piémont nord-pyrénéen (comptages polliniques

réalisés par J.-P. Suc, G. Jiménez-Moreno, S. Popescu). Les sédiments prélevés couvrent environ 58 Ma, ce qui va nous permettre de suivre l'histoire des paléoreliefs au cours du temps tout au long de la chaîne depuis le début du Paléocène (Fig. 38 et 39). Toutefois, un grand nombre d'échantillons prélevés se sont avérés stériles, en particulier aucun échantillon ne permet de couvrir la période comprise entre ~25 et 45 Ma (Fig. 39).



Fig. 38. Carte de localisation des échantillons prélevés pour l'analyse pollinique.

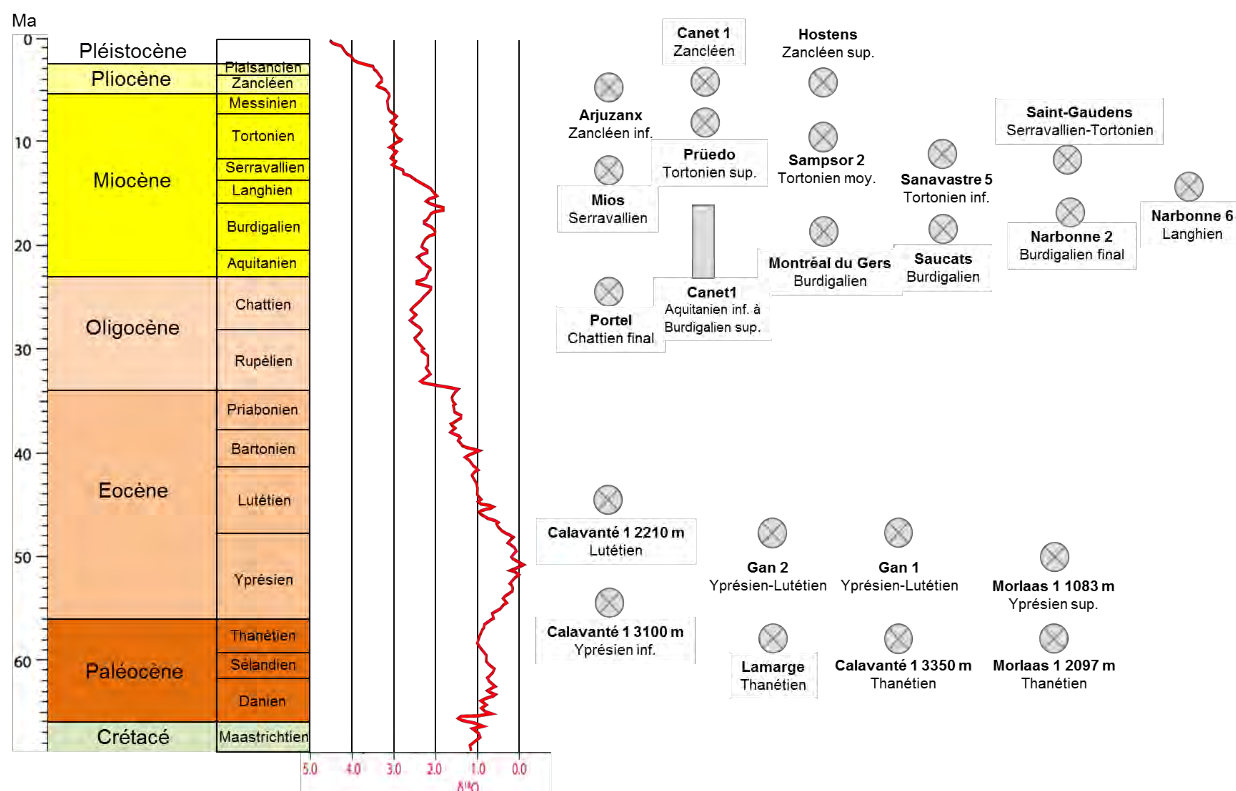


Fig. 39. Position chronostratigraphique des échantillons polliniques du bassin Nord-Pyrénéen et de Cerdagne.

Les premiers résultats montrent qu'entre *le Thanétien et le Lutétien* (~58 à 45 Ma) les données polliniques mettent en évidence la présence de plantes subtropicales, voire tropicales, à basse altitude et d'arbres tempérés-froids (*Podocarpus*, *Cathaya*) dans l'arrière-pays.

Pour ces périodes anciennes, les seules plantes indiquant des reliefs ne se trouvent plus actuellement en Europe (*Podocarpus*, *Cathaya*). On ne peut donc pas utiliser les méthodes de quantification des paléoaltitudes que j'ai utilisées jusqu'à présent. Dans ce cas, il va falloir rechercher leur répartition altitudinale actuelle sous un climat équivalent au climat que l'on estimera d'après les données polliniques puis en déduire une paléoaltitude approximative des reliefs.

C'est à partir de l'Aquitanién inférieur (~22 Ma) que l'on voit apparaître le sapin et l'épicéa, arbres microthermes toujours présents à haute altitude dans les Pyrénées de nos jours. On pourra donc, à partir de cette période, appliquer la méthode de quantification des paléoaltitudes.

Pour le moment, le manque de données entre 45 et 25 Ma ne nous permet malheureusement pas de connaître le timing précis de l'évolution des paléoaltitudes. Des forages, proches de la chaîne pyrénéenne, couvrant cette période existent (Marpaps 1, Pomps 1 par exemple; Sztrakos et al., 1998) et pourraient permettre de combler cette lacune. De même, la rareté des flores au sud de la chaîne ne permet pas dans un premier temps de valider l'hypothèse d'une dissymétrie climatique nord-sud. Il faudra réaliser des études similaires sur le versant sud des Pyrénées.

3 - Etendre mes recherches dans le temps et dans l'espace

Paléoenvironnements en zone arctique au Paléogène

Le visage actuel de l'océan Arctique s'est ébauché dès le Paléogène avec l'ouverture du bassin eurasién. A l'Eocène, l'océan Arctique était un vaste bassin isolé des autres bassins océaniques et entouré de larges surfaces continentales, la connexion du bassin eurasién avec l'Atlantique Nord se fait au cours du Miocène.

Les premières données du forage IODP 302 ACEX sur la dorsale de Lomonosov (Fig. 40 ; Moran et al., 2006) nous indiquent qu'à cette même période, l'environnement arctique subissait des changements climatiques dramatiques depuis les maxima thermiques paléocènes-éocènes vers un système englacé sans doute dès l'Eocène moyen et que l'Éocène inférieur est marqué par une sédimentation particulièrement enrichie en matière organique (*black shales*) dans le centre du bassin.

Le Paléocène et le début de l'Eocène, entre ~56 et 50 millions d'années, sont connus comme étant les périodes les plus chaudes du Cénozoïque, avec une phase chaude rapide, le *Late Paleocene Thermal Maximum* (LPTM) à la limite Paléocène-Eocène (~57 Ma), et un maximum thermique au début de l'Eocène, le *Early Eocene Climatic Optimum* (EECO), entre 52 et 50 Ma (Zachos et al., 2001). Ces périodes chaudes sont certainement dues à de fortes concentrations en CO₂ atmosphérique (Sloan et Barron, 1992). A partir de 49 Ma, le climat semble être marqué par un refroidissement constant avec, à partir de l'Eocène moyen (~45 Ma), la détection dans les sédiments d'Ice-Rafted Debris (IRD) indiquant la présence de glace sur le pôle (Moran et al., 2006).

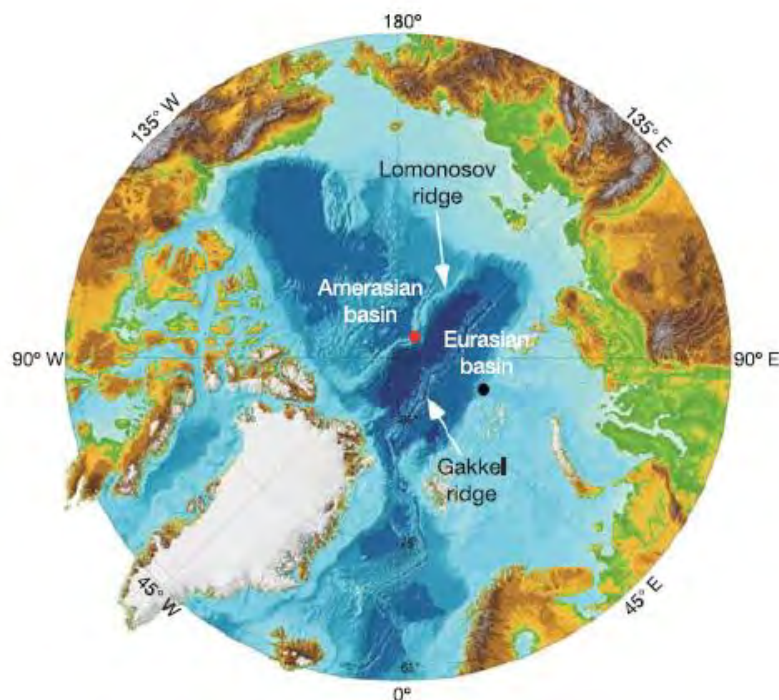


Fig. 40. Localisation du forage IODP 302 ACEX (point rouge) sur la dorsale de Lomonosov. Le point noir indique sa paléoposition (d'après Moran et al., 2006).

Différentes données couvrant l'EEOC indiquent des températures très élevées, aussi bien pour les températures de surface des eaux que pour les températures de l'air (*e.g.* Pross et al., 2012; Sluijs et al., 2006; Weijers et al., 2007). Mais ces températures ne peuvent être reproduites par les modèles climatiques que s'ils fixent des concentrations de CO₂ extrêmement élevées (>4000 ppm !), bien au-dessus des valeurs reconstituées à partir des données de terrain (Huber and Caballero, 2011; Lunt et al., 2012).

L'EEOC est donc un intervalle qu'il faut étudier plus précisément afin d'obtenir des reconstitutions climatiques plus fines et de calibrer les modèles climatiques sur des périodes, passées ou futures, où les taux de CO₂ sont plus élevés qu'actuellement.

Dans ce cadre, une première étude a été réalisée sur des sédiments prélevés sur des coupes sur les îles de Nouvelle-Sibérie en mer de Laptev, au Nord de la côte sibérienne : sur l'île de Belkovsky (75°30'16,7" / 135°59'07,4") et de Faddeevsky (76°06'23,3" / 141°49'01,7"). Dans cette étude, des analyses géochimiques, palynologiques et des reconstitutions climatiques ont été réalisées (Suan et al., soumis). Les assemblages polliniques (Fig. 41) ont mis en évidence une flore exceptionnellement riche en taxons subtropicaux et même tropicaux, en particulier des palmiers, *Avicennia* (mangrove) et *Bombax*, qui vivent uniquement dans les régions qui ne connaissent pas de période de gel. Les estimations climatiques que j'ai obtenues en appliquant sur les données polliniques la méthode des amplitudes climatiques (Fauquette et al., 1998 a, b), montrent des températures et des précipitations très élevées (Ta entre 14 et 21°C, Pa entre 1100 et 1200 mm) pour le début de l'Eocène (coupe de Faddeevsky) et des températures et des précipitations un peu plus basses (Ta entre 12 et 18°C, Pa entre 950 et 1100 mm) pour la deuxième coupe plus jeune (Belkovsky) (Fig. 41 ; Suan et al., soumis).

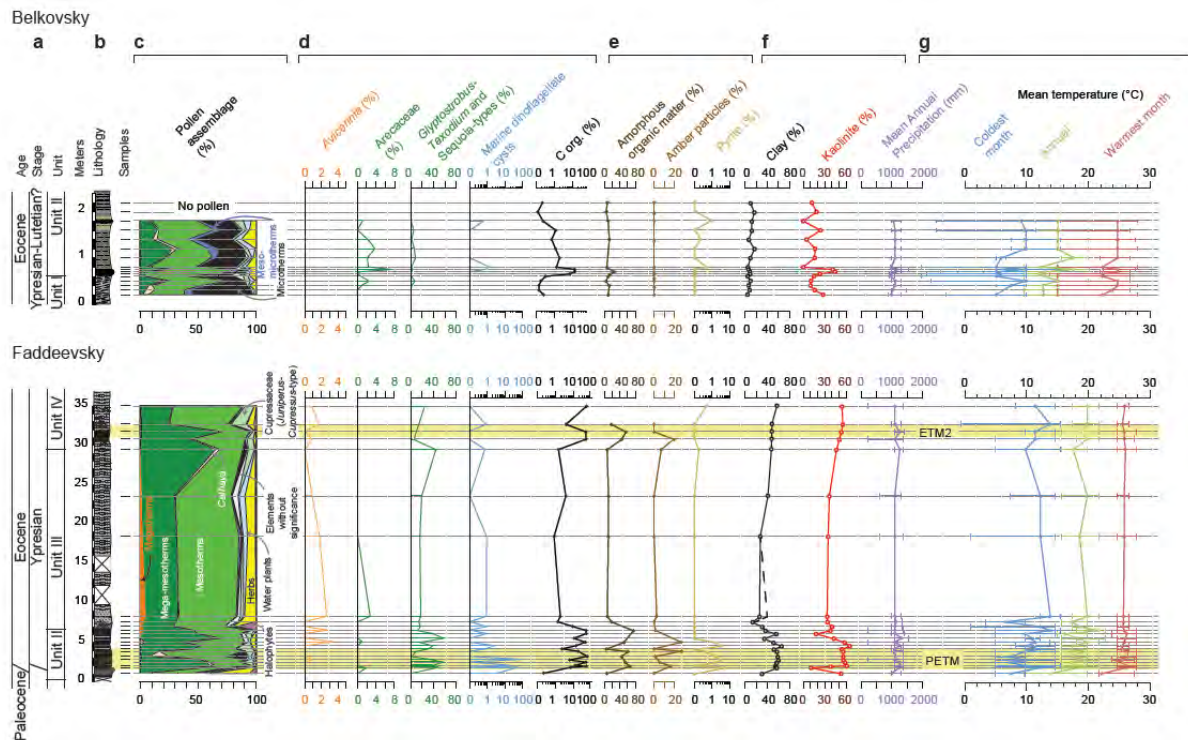


Fig. 41. Palynologie, minéralogie et climat pour les coupes Eocènes Faddeevsky et Belkovsky en Nouvelle-Sibérie (d'après Suan et al., soumis).

Les valeurs obtenues pour Faddeevsky sont en accord avec les fortes proportions en kaolinite dans les sédiments (>40%). De telles proportions sont de nos jours trouvées dans des sols sous latitudes subtropicale et tropicale (Griffin et al., 1968) caractérisées par des températures annuelles supérieures à 15°C et des précipitations supérieures à 1000 mm (Robert and Kennett, 1994). Les précipitations annuelles élevées impliquent un apport très important dans l'océan Arctique éocène d'eau douce chaude ce qui va élever les températures des eaux de surface, ce qui entraîne probablement, parmi d'autres facteurs, le réchauffement de la zone polaire (Whitefield et al., 2015). Par ailleurs, ces conditions climatiques singulières, associées à une circulation océanique restreinte, sont considérées comme les principales causes de l'accumulation de sédiments riches en matière organique au centre du bassin Arctique.

➤ Dans ce cadre, un projet déposé auprès de l'INSU (GDR Marges, porteur : G. Suan, Laboratoire de Géologie de Lyon Terre, Planètes, Environnement) propose de produire de nouvelles reconstitutions géographiques et climatiques de l'Arctique à l'Éocène inférieur à partir de données palynologiques, géochimiques et minéralogiques de deux autres localités-clé de cette région. Les sites d'étude sont localisés sur la bordure du bassin de Beaufort-Mackenzie (Canada, au Nord du Cercle Polaire, 68-69°N) et sur la ride de Lomonosov (IODP 302 ACEX) (Fig. 42). Les reconstitutions des températures et des précipitations seront réalisées à partir des analyses bioclimatiques des spectres polliniques de chacun des sites comme nous l'avons déjà fait pour la Nouvelle-Sibérie.

Ces analyses permettront de confirmer ou de réfuter l'hypothèse selon laquelle une végétation de type subtropical caractérisait l'ensemble de l'Arctique lors de cette période et de mieux contraindre l'évolution paléogéographique du bassin ; à terme, il s'agira de mettre à l'épreuve les différents modèles climatiques et paléogéographiques proposés pour le bassin Arctique à l'Éocène inférieur.

L'étude du bassin de Beaufort-Mackenzie a débuté puisque deux séries d'échantillons ont été prélevées le long des affleurements de Caribou Hills (Fig. 42). Les échantillons sont en cours d'analyse (thèse en cours à l'ISTEP, M. Salpin) afin d'étudier la minéralogie, la matière organique, les isotopes du carbone et les pollens.

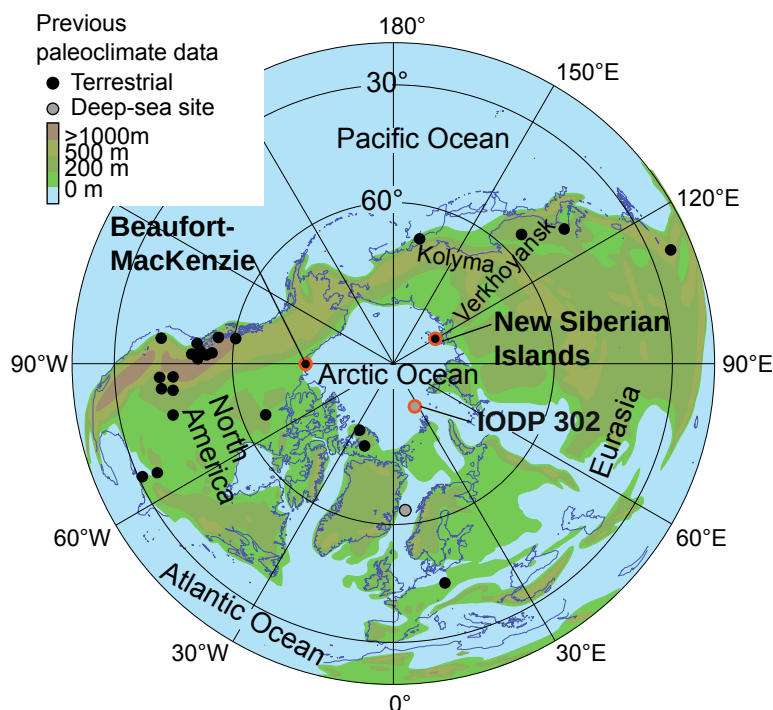


Fig. 42. Localisation des coupes du bassin de Beaufort-MacKenzie et de Nouvelle-Sibérie, et de l'IODP 302.

4 - Conclusion

Depuis le début de ma carrière, mon thème de recherche concerne les conditions d'évolution et de la mise en place de la diversité végétale en Méditerranée et en Europe afin de connaître la part respective de l'influence des changements du climat, des taux de CO₂, de la tectonique et de l'action anthropique sur la végétation.

Dans ce cadre, mon activité de recherche principale portait jusqu'à présent sur la quantification du climat du Néogène en région Méditerranéenne et en Europe, l'étude de l'évolution de la diversité végétale en relation avec les fluctuations des facteurs forçants (climat, CO₂, tectonique) depuis le début du Néogène, et enfin sur l'estimation des paléoaltitudes pour une meilleure modélisation du climat.

Actuellement je poursuis ces études avec d'autres projets que je n'ai pas détaillés ici, en particulier des reconstitutions paléoenvironnementales dans les Alpes du Nord (région du Mont-Blanc), dans le Massif Central (Plomb du Cantal).

➡ Pour les années à venir, je fais le choix de rester sur cette même voie mais en élargissant mes recherches sur des zones géographiques et/ou des périodes de temps différentes qui sont moins bien connues et qui pourtant jouent un rôle indéniable dans l'évolution des systèmes climatique et écologique de notre planète.

Ces travaux ne se feront pas sans l'amélioration de la base de données des amplitudes climatiques supportées par les plantes, sans travaux de calibration entre données polliniques et végétation, en particulier dans mes nouvelles zones d'étude, et sans une réflexion plus théorique sur l'utilisation des méthodes de reconstitution des paléoenvironnements. Par exemple :

- jusqu'à quelle période de temps peut-on remonter raisonnablement ?
- Est-ce que les exigences climatiques des plantes ont varié dans le temps ?

Par ailleurs, les travaux prévus dans certains de ces projets, en particulier le projet sur l'Amérique du Sud, seront réalisés par des étudiants, d'abord en Master afin de tester la faisabilité du projet puis en thèse compte-tenu de l'étendue des études à réaliser (données palynologiques sur plusieurs sites contemporains à différentes altitudes, calibrations sur l'actuel, interprétations paléoécologiques, quantifications).

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Fig. 1. $\delta^{18}\text{O}$ (‰) de l'océan global basé sur la compilation de plus de 40 sites ODP et DSDP et principaux événements climatiques et tectoniques (modifié d'après Zachos et al., 2001).

Fig. 2. Flores polliniques couvrant le Néogène (Miocène et Pliocène) en Europe de l'Ouest et région méditerranéenne.

Fig. 3. Projection des taxons actuels étudiés sur un climagramme (modifié d'après Fauquette et al., 1998b).

Fig. 4. Superposition des exigences climatiques de plusieurs taxons afin d'en inférer une estimation climatique sous forme d'intervalle [R- ; R+] et d'une valeur moyenne pondérée (Fauquette et al., 1998 a, b).

Fig. 5. Répartition en altitude des groupements végétaux en fonction de la latitude (d'après Troll, 1973).

Fig. 6. Variation altitudinale de l'étage du hêtre (a) et du sapin/épicéa (b) en fonction de la latitude en Europe de l'Ouest.

Fig. 7. Méthode de reconstitution de la paléoélévation d'un site continental (modifié d'après Suc et Fauquette, 2012).

Fig. 8. Localisation des sites de Tongres et Montauban (carte paléogéographique de Meulenkamp et Sissingh, 2003).

Fig. 9. a. Données polliniques du Miocène moyen (~15 Ma) dans le Sud-Ouest de l'Europe (d'après Jiménez-Moreno, 2005 ; Jiménez-Moreno et al., 2010 ; Fauquette et al., 2007). Carte paléogéographique du début de Serravallien d'après Rögl (1998). b. Reconstitution des températures et précipitations annuelles (Fauquette et al., 2007).

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Fig. 21. Diagrammes polliniques synthétiques ayant permis de reconstituer la végétation, le climat et les paléoaltitudes des Alpes depuis la fin de l'Eocène jusqu'au Pléistocène (d'après Fauquette et al., 2015a).

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Fig. 23. Géologie régionale, localisation et diagrammes polliniques des séquences de Sanavastre/Sampson (1), Can Vilella (2) et le Boulou (3) (modifié d'après Suc et Fauquette, 2012).

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Annexe

Sélection de publications

- Fauquette S.**, Guiot J., Suc J.-P., 1998. A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 144 (1-2), 183-201.
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PALAEO

A method for climatic reconstruction of the Mediterranean Pliocene using pollen data

S  verine Fauquette ^{a,*}, Jo  l Guiot ^a, Jean-Pierre Suc ^b

^a Institut M  diterran  en d'Ecologie et de Pal  o  cologie (ERS CNRS 6100), case 451, Facult   des Sciences de Saint-J  r  me, Avenue Escadrille Normandie-Niemen, 13297 Marseille cedex 20, France

^b Centre de Pal  ontologie stratigraphique et Pal  o  cologie (UMR CNRS 5565), Universit   Claude Bernard, Lyon 1, 29 boulevard du 11 Novembre, 69622 Villeurbanne cedex, France

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Abstract

Pollen data from numerous sites around the Mediterranean Sea indicate that several important vegetation and climatic changes occurred during the Pliocene. These data are in good agreement with pollen records from northwest Europe and with $\delta^{18}\text{O}$ curves from Mediterranean and Atlantic deep-sea cores. Quantitative palaeoclimatic reconstructions from Pliocene pollen data of the Mediterranean region cannot be based on conventional modern analogue techniques, as individual Pliocene pollen spectra contain taxa representing temperate, warm-temperate and subtropical plants that do not grow together today. Instead, we propose a new method that uses a climatic amplitude method modified to take partially into account the relative abundances of the taxa. We applied this method to the Pliocene Garraf 1 palynological sequence from Catalonia, which provides a long continuous record of climatic change from 5.3 Ma to the Early Pleistocene. We estimate that annual temperatures were 1 to 5  C higher than today and the annual precipitation 400 to 1000 mm higher than today prior to the beginning of the late Cenozoic glacial–interglacial cycles. In contrast, temperature and precipitation both fell sharply during the glacial phases of the earliest glacial–interglacial cycles.    1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

During the Pliocene mid-latitude environments changed from tropical and subtropical to near-modern conditions (Zagwijn, 1960; Axelrod, 1973; Suc, 1984; Pons et al., 1995). This period is particularly well-documented in pollen records from western and southern Europe. The Mediterranean and nearby re-

gions provide several continuous Pliocene pollen sequences (Cravatte and Suc, 1981; Suc and Cravatte, 1982; Bessais and Cravatte, 1988; Drivaliari, 1993; Bertini, 1994; Drivaliari et al., 1998). The main climatic events identified using pollen records are fully consistent with those defined using the $\delta^{18}\text{O}$ deep-sea records (Tiedemann et al., 1994; Shackleton et al., 1995) and also Mediterranean $\delta^{18}\text{O}$ records (Vergnaud Grazzini et al., 1990; Thunell et al., 1990). In addition to their variability in time, Mediterranean Pliocene pollen diagrams show a high

* Corresponding author. Tel.: +33 (491) 288524; Fax: +33 (491) 288668; E-mail: severine.fauquette@lbhp.u-3mrs.fr

degree of spatial variability (Suc, 1989; Suc et al., 1995a), and the overall geographic pattern is more or less similar to the modern pattern (Suc et al., 1995a,b). Consequently, the area appears very propitious to Pliocene climatic quantification with the aim of testing general circulation models such as the GISS model which has been run for this period (Crowley, 1991; Chandler et al., 1994). Dowsett et al. (1992) have emphasised the importance of the last Pliocene climatic warming at 3.1 Ma before the onset of glacial–interglacial cycles (at 2.6 Ma) for providing insights into possible future climatic conditions under a warmer-than-modern ‘greenhouse’ climate. This middle Pliocene warm period is well documented in the Mediterranean region.

Pliocene pollen spectra from the Mediterranean region include many taxa still extant in Europe and the circum-Mediterranean areas (for example, *Quercus*, *Olea*, *Cistus*), in addition to subtropical elements (for example, *Taxodiaceae*, *Engelhardia*, *Symplocos*) that no longer live in these regions. These combinations of pollen taxa cannot be found occurring together in the modern landscape, thus precluding the use of the best analogue method for climatic reconstruction (Guiot, 1990). Consequently, it is necessary to devise an alternative method, which does not need any analogue, to reconstruct the climate of this period. The method proposed here uses the climatic requirements of a few modern taxa to interpret the fossil data. Although other researchers have attempted similar studies (Zagwijn, 1975; Mai, 1995; Suc et al., 1995b), this is the first large-scale systematic attempt to reconstruct Pliocene climates from modern floral vegetation/climate relations.

Our method involves two steps: (1) determination of the precise climatic ranges of a few key plants of the Mediterranean Pliocene, including both extirpated subtropical plants and plants that still live in the region (Fauquette et al., 1998a), and (2) determination of the climatic amplitudes of various pollen-taxa on the basis of several thousand pollen modern spectra. In contrast with the best analogue method (Guiot, 1990), this approach does not rely on the analysis of entire pollen assemblages, but rather on interpreting the pollen abundance of each individual taxon in relation to climate. Such a type of method was developed by Iversen (1944) to quantify the post-glacial climate from a few indicator

plant species and by Atkinson et al. (1986), who took their inspiration from Grichuk (1969), to quantify the palaeoclimatic interpretations of Quaternary coleoptera. These last authors called the method the ‘Mutual Climatic Range Method’ that is based on the establishment of the range of climates occupied at the present-day by beetle species represented in a fossil assemblage.

Here, we present first the full description of this new quantitative pollen-derived palaeoclimatic reconstruction. In a second part, we present its application to a Pliocene marine pollen record (Garraf 1 core, Suc and Cravatte, 1982). The palaeoclimatic interpretations from this core are then compared with the climatic changes seen in deep-sea $\delta^{18}\text{O}$ curves (Thunell et al., 1990; Vergnaud Grazzini et al., 1990; Tiedemann et al., 1994) and to the values obtained by transfer functions based on marine (Dowsett and Poore, 1991; Edwards et al., 1991) or continental (Montuire, 1994; Michaux et al., 1996; Aguilar et al., 1998) faunas.

2. Modern data and method

2.1. Taxa still living in Europe and in the Mediterranean region

Almost 8000 modern pollen spectra were used in the statistical part of the method. These spectra correspond to surface samples or core-tops which were collected in the Northern hemisphere, in Eurasia and in North America and then compiled by B. Huntley, P.J. Bartlein, (pers. commun.) and Peyron et al. (1998). They represent a great diversity of vegetation and sedimentary environment types, and thus of climates. These modern pollen spectra allow us to include in our analysis a range of climates from northern boreal to warm-temperate conditions.

The values of the modern climatic parameters corresponding to each sampling site have been provided by B. Huntley (pers. commun.) according to the following procedure: (1) mean monthly values, of temperature, precipitation and cloudiness were interpolated using Laplacian thin-plate spline surfaces (Hutchinson, 1989), (2) bioclimatic variables [temperatures of the coldest and warmest months, E/PE (the ratio of actual evapotranspiration to po-

tential evapotranspiration), GDD5 (growing degree-days above 5°C)] were calculated with the biome 1 model of Prentice et al. (1992), using the monthly interpolated meteorological values.

Pollen percentages were calculated for each spectrum, based on the total pollen sum, but excluding pollen of water-plants and spores. Cyperaceae pollen is included in the pollen sum.

Six climatic parameters were considered: mean annual temperature (T_A), total annual precipitation (P_A), mean temperature of the coldest month (T_C), mean temperature of the warmest month (T_W), available moisture (i.e. the ratio of actual evapotranspi-

ration to potential evapotranspiration, E/PE), and growing degree-days above 5°C (GDD5). These parameters are, for the major part, considered by Woodward (1987) and Prentice et al. (1992) as the most important variables in determining plant distributions. The modern climatic amplitude tolerated by each pollen taxon was determined by plotting pollen percentages of each taxon in the modern pollen spectra in relation to each climatic parameter (Fig. 1). Such graphs were made for many taxa and were analysed in the following manner.

On each graphical display, we defined, visually, one or two thresholds (Fig. 1): the first one cor-

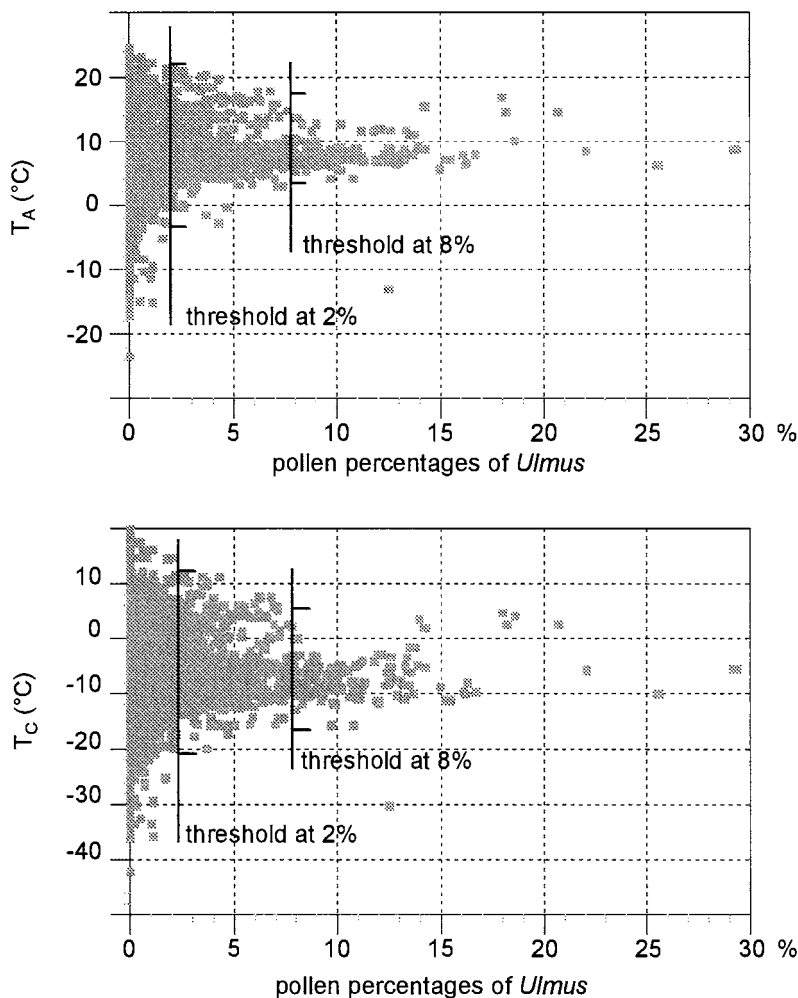


Fig. 1. Pollen percentages distribution of *Ulmus* as a function of T_A and T_C (°C). Each grey point corresponds to a surface pollen spectrum for which the values of the different climatic parameters are known. The vertical black lines correspond to the thresholds which can be defined according to the refined climatic limits of the taxon when percentages increased.

responds to the presence/absence threshold under which the taxon is probably not at the site (pollen percentages below this level reflect long-distance transport by wind or water); the second one corresponds to the abundance threshold. Sometimes a third threshold is defined, reducing again the amplitude of almost one of the parameters. Each of these thresholds are taxon-dependent and may be different for each taxon. In a given pollen spectrum (modern or fossil), if the percentage of a taxon exceeds 80% of the first (lower) threshold, then the climatic amplitude associated with that threshold is used in the reconstruction. If the percentage of the taxon exceeds 80% of the second (upper) threshold, then the more restricted climatic amplitude associated with that threshold is used also. Values of T_C , T_W , GDD5 and available moisture have been homogenised with those given by Prentice et al. (1992) according to the plant functional type. For example, the minimum tolerated value of available moisture of sclerophyll plants corresponds to 28% (Prentice et al., 1992).

Of course, the so-obtained climatic ranges are not real physiological values. The obtained values depend in part on the method used to define the intervals and also on the diversity of the modern data set. The way of determination of the climatic conditions tolerated by these plants, based on pollen data, does not allow to consider the extreme cases of endurance of the plants, because modern pollen spectra have not been collected from all parts of the earth.

For the calculation of palaeoclimatic estimates for low and middle-low altitude Pliocene sites, the pollen taxa have been separated into three groups: a group (U) of ubiquitous (at the genus level) taxa (for example *Quercus* deciduous type); a group (C) of taxa growing in cold regions (at high altitudes and/or high latitudes, for example *Picea*, *Abies* etc.); a third group (W) of taxa growing in warm regions (at low altitudes and/or low latitudes, for example *Arbutus*, *Quercus* evergreen type, *Zizyphus* etc.). For pollen taxa such as Poaceae and Cyperaceae for which we cannot determine the species or even the genus, two climatic ranges have been defined on the graphs, one for taxa growing in cold regions and a second for taxa growing in warm regions.

All these values (thresholds, groups and climatic amplitudes) are given in Table 1 which provides the key data for climate reconstructions. For a given

spectrum, each taxon exceeding its threshold(s) provides a climatic range which was compared to those obtained for the other taxa. The most probable climatic range for the spectrum was provided by the smallest climatic range suitable for the maximum of taxa (i.e. the likely interval [R_- ; R_+]) (Fig. 2). If the reconstructed climatic interval was too small (i.e. less than 5% of the maximum climatic range) and thus had a low level of probability, the lower and upper limits were extended to the next smaller interval (i.e. the enlarged interval [R'_- ; R'_+]).

For each Pliocene sample, two different histograms were considered: one with ubiquitous and cold plants (high altitude) and another with ubiquitous and warm plants (low altitude). We then calculated a 'most likely value' which corresponded to a weighted mean in relation to the inverse of the external surface of the histogram (below R_- and above R_+):

$$R_0 = \frac{\frac{R_-}{SI} + \frac{R_+}{SS}}{\frac{1}{SI} + \frac{1}{SS}}$$

where R_- is the lower limit of the likely interval, R_+ is the upper limit, SI the inferior surface (below R_-), SS the superior surface (above R_+) (Fig. 2). We imposed two conditions: R_0 was necessarily included in the likely interval, and in the case where the interval has been enlarged to the lower probability level (between R'_- and R'_+ , Fig. 2), R_0 was constrained to be in the restricted interval [R'_- ; R'_+].

This way of calculation allows us to give more weight to the subtropical taxa when they are relatively numerous, as in the case of subtropical fossil spectra. A small external surface gives more precise information concerning the limits of the climatic ranges, whereas a large external surface implies a probable mixture of non-compatible pollen taxa in a single assemblage.

2.2. Marker-taxa of the Mediterranean Pliocene

Some important 'marker'-taxa cannot be studied in the same way because of the lack of modern subtropical pollen spectra that contain the Pliocene pollen taxa. Instead, we estimated the modern climatic ranges of subtropical taxa by examining their

Table 1

Plant type (U, W or C plants), thresholds (the first value corresponding to the presence/absence threshold, and the second one to the abundance threshold) and climatic amplitudes (minimum and maximum values for the six chosen climatic parameters) of some taxa still living in Europe and the Mediterranean region and of some 'exotic taxa'

Taxa	Type	Thresholds (%)	T_A (°C)		T_C (°C)		T_W (°C)		P_A (mm)		E/PE (%)		GDD5 (degr. days)	
<i>Abies</i>	C	5	−6.0	13.0	−20.0	10.0	6.0	26.0	600	1600	66	100	350	3000
	C	25	0.0	11.0	−16.0	4.0	10.0	24.0	600	1600			350	3000
<i>Acer</i>	U	2			−20.0	13.0					66	100	500	5600
	U	6	0.0	18.0	−16.0	10.0	16.0	27.0	750	1400	85	100	1000	5000
	U	8	4.0	16.0	−11.0	6.0	18.0	26.0	750	1400	90	100	1500	3900
<i>Alnus fruticosa</i>	C	2	−12.5	−4.0	−35.0	−30.0	12.0	20.0		500			350	1000
<i>Alnus</i>	U	10											350	4200
<i>Arbutus</i>	W	0.5	8.0	18.0	−5.0		19.0	26.0	550	1600	28	90	1000	5000
<i>Artemisia</i>	C	5	−17.5	5.0					100	700	18	64	0	500
	W	5	−2.5	20.0					100	700	18	64	500	5800
	C	15			−35.0	−25.0	2.5	12.5						
	W	15			−25.0	5.0	17.5	27.5						
<i>Betula nana</i>	C	2	−13.0	0.0	−35.0	−12.0	10.0	20.0		500			350	1500
<i>Betula</i>	U	5	−8.0	12.5							66	100	350	2500
	U	25		12.5	−30.0	−5.0					66	100	350	2500
	U	35			−30.0	−5.0	12.0	22.5	200	700				
	U	35					12.0	22.5	900	1700				
<i>Buxus</i>	W	3	9.0	12.0	−2.0	4.0	18.0	24.0	600	1000	65	75	2000	3200
<i>Calligonum</i> #	W	0.5	16.0	24.0	10.0	15.0	20.0	35.0	40	100	18	64	3800	7150
<i>Carpinus</i>	W	2.5							600	1300	66	100		
	W	5	4.0	25.0	−7.0	6.0	14.0	27.0	600	1100	66	100	1000	4200
	W	15	6.0	17.0			17.0	27.0					1600	4100
<i>Castanea</i>	U	5	6.0	17.0	−5.0	9.0	15.0	25.0	600	1450	66	100	1600	3500
	U	20	9.0	14.0	−1.0	3.0	18.0	23.0	600	950	66	100	2600	3300
<i>Cathaya</i> #	W	0.5	10.0	20.0	5.0	10.0	15.0	30.0	1000	1600	66	100	1350	5500
<i>Cedrus</i>	U	5	7.0	18.0	−1.0	11.0	18.0	28.0	500	1500	66	100	1600	4900
	U	25	8.0	13.0	1.0	5.0	17.0	23.0	750	1250	66	100	900	8000
<i>Centaurea</i>	U	2	10.0	25.0	−3.0	2.0	21.0		500	1000	18	64	1500	
<i>Ceratonia</i> #	W	0.5	17.0	22.0	5.0	15.0	20.0	30.0	500	900	18	64	3400	6300
Chenopodiaceae	U	10	−12.0	25.0	−25.0	20.0	8.0	35.0	50	1600	18		500	
	U	40	0.0	25.0	−13.0	20.0	13.0	35.0	50	1600	20	95	1000	7000
<i>Cistus</i>	W	5	11.0	25.0	2.0		20.0		300	1000	28		1500	
	W	10	14.0	25.0	4.0		24.0				28		3000	
Composae liguliflorae	U	2	10.0	25.0	−3.0		20.0		300	1300	18	64	1500	
	U	15	16.0	25.0	8.0		22.0		300	700	18	64	1500	
Composae tubuliflorae	U	2					16.0	28.0	300	1300	18	64	500	
	U	6						28.0	350	900	18	64	500	
	U	8	10.0		−3.0	6.0	21.0	30.0	350	900			1500	
	U	10	10.0		7.0	15.0	22.0	30.0	250	700			1500	
<i>Corylus</i>	U	5	0.0	18.0	−15.0	12.0	10.0	27.0	550		66	100	900	
	U	15	5.0	13.0	−10.0	7.0	13.0	23.0	550	1550	71	100	900	3300
Cyperaceae	W	20	−4.0	25.0	−15.0	20.0			100	2000	18	100		
	C	20	−16.0	−5.0	−40.0	−18.0			100	2000	18	100	100	500
<i>Carpodiptera</i> #	W	0.5	20.0	26.0	15.0	25.0	26.0	29.0	1400	2800	66	100	5550	7750
<i>Distylium</i> #	W	0.5	15.0	25.0	10.0	20.0	25.0	35.0	800	2000	66	100	3700	7800
<i>Engelhardia</i> #	W	5	15.0	25.0	10.0	20.0	25.0	35.0	800	2000	66	100	3150	7800
<i>Ephedra</i>	U	5	2.0	20.0	−20.0	15.0	17.0	27.0	200	800	10	55	1500	5300
	U	15	10.0	17.0	−2.0	14.0	22.0	27.0	250	350	18	35	2300	4700
<i>Ephedra fragilis</i>	W	2	14.0	20.0	5.0		23.0	28.0	200	700	18	55	2500	6000
Ericaceae	U	10							50	1600	28	100		

Table 1 (continued)

Taxa	Type	Thresholds (%)	T _A (°C)	T _C (°C)	T _W (°C)	P _A (mm)	E/PE (%)	GDD5 (degr. days)		
	U	20	−12.0	20.0	−33.0	12.0	5.0	24.0	350	4400
	U	45	−2.0	16.0	−15.0	11.0	8.0	24.0	600	1200
Euphorbiaceae	W	1	10.0	20.0	0.0		20.0		200	1200
Fabaceae	U	2	4.0	20.0	−20.0		8.0		200	1500
	U	10	11.0	20.0	4.0		22.0	28.0	200	800
<i>Fagus</i>	U	5	−3.0	15.0	−15.0	7.0	10.0	27.0	600	1800
	U	20	−1.0	13.0	−13.0	4.0	10.0	22.0	600	1300
<i>Fraxinus excelsior</i>	U	5	3.0	25.0	−15.0	13.0	14.0	27.0	400	1600
	U	10	3.0	25.0	−11.0	11.0	15.0	27.0	400	1600
	U	15	8.0	21.0	−5.0	12.0	22.0	27.0	1000	1600
<i>Humulus</i>	W	0.5	8.0	16.0	−1.0	10.0	19.0	28.0	550	1350
<i>Juglans</i>	U	5	4.0	20.0	−11.0	11.0	18.0	27.0	600	1400
	U	10	7.0	16.0	−8.0	6.0	20.0	27.0	600	850
<i>Juniperus</i>	W	5	1.0	25.0	−15.0	20.0	9.0	31.0		
<i>Keteleeria</i> #	W	0.5	16.0	23.0	5.0	10.0	21.0	28.0	1000	2000
<i>Larix</i>	C	1			−28.0	0.0	7.0	24.0	600	1400
	C	2	−10.0	10.0	−28.0	0.0	7.0	24.0	600	1100
<i>Liquidambar</i> #	W	0.5	10.0	23.0	0.0	18.0	20.0	30.0	1000	1600
<i>Lygeum</i> #	W	0.5	16.0	25.0	5.0	15.0	20.0	30.0	150	400
<i>Microtropis fallax</i> #	W	0.5	22.0	25.0	15.0	19.0	25.0	29.0	1700	2500
<i>Myrtus</i>	W	0.5	16.0	25.0	6.0		24.0		300	900
<i>Neurada</i> #	W	0.5	15.0	25.0	10.0	15.0	20.0	35.0	20	200
<i>Nitraria</i> #	W	0.5	18.0	25.0	10.0	15.0	20.0	35.0	50	150
<i>Nolina</i> #	W	0.5	17.0	25.0	8.0	23.0	23.0	35.0	200	600
<i>Nyssa</i> #	W	0.5	18.0	25.0	10.0	25.0	24.0	35.0	900	2400
<i>Olea</i>	W	5	3.0	21.0	−6.0	15.0	14.0	32.0		
	W	10	3.0	21.0	−6.0	15.0	14.0	32.0	100	1300
	W	35	14.0	18.0	6.0	13.0	18.0	27.0	300	850
<i>Ostrya</i>	W	1	−3.0	21.0	−16.0	15.0	12.0	28.0	400	1650
	W	8	3.0	15.0	−13.0	7.0	13.0	24.0	400	1650
<i>Parrotiopsis jacquemontiana</i> #	C	0.5	7.0	13.0	−7.0	3.0	17.0	24.0	300	1000
<i>Parrotia persica</i> #	W	0.5	14.0	20.0	4.0	8.0	24.0	35.0	300	1500
<i>Phillyrea</i>	W	2	10.0	25.0	1.0	20.0	18.0	27.0	250	1400
	W	10	13.0	20.0	1.0	20.0	22.0	27.0	300	1100
<i>Phlomis fruticosa</i> #	W	0.5	15.0	20.0	5.0	15.0	20.0	30.0	400	800
<i>Picea</i>	C	5	−16.0	14.0			3.0	23.0	600	2450
	C	20	−14.0	10.0	−35.0	3.0	3.0	23.0	600	2450
	C	50	−10.0	10.0	−35.0	3.0	10.0	23.0	600	1600
<i>Pinus haploxylon</i>	C	5	−15.0	−5.0	−40.0	−22.0	8.0	18.0		600
<i>Pistacia</i>	W	3	11.0	25.0	−2.0	13.0	21.0	30.0	200	1400
	W	35	11.0	25.0	−2.0	13.0	21.0	30.0	350	650
<i>Platanus</i>	W	2	5.0	19.0	−10.0	10.0	16.0	31.0	350	1400
	W	5	10.0	17.0	−2.0	13.0	22.0	30.0	600	1400
<i>Platycarya</i> #	W	0.5	10.0	20.0	−5.0	15.0	15.0	28.0	1000	2400
<i>Plumbago</i>	W	0.5	13.0	25.0	2.5		23.0	30.0	200	600
Poaceae	C	25	−17.5	5.0	−45.0	−25.0	2.5	12.5	100	700
	W	25	−2.5	−15.0	15.0		17.5	27.5	100	1300
<i>Quercus deciduous type</i>	C	5	3.0	−20.0	20.0		7.0	31.0	600	1900
	C	20	5.0	23.0	−14.0	20.0	13.0	30.0		
<i>Quercus ilex type</i>	W	53.0	25.0	−6.0	15.0		13.0	30.0	250	1200
	W	20	9.0	25.0	−3.0	12.0	17.0	28.0	250	1200
<i>Rhamnus</i>	W	0.5	9.0	20.0	−2.0		19.0	27.0	300	1000
<i>Rhus</i>	W	0.5	15.0	22.0	5.0		23.0	26.0	300	900

Table 1 (continued)

Taxa	Type	Thresholds (%)	T_A (°C)	T_C (°C)	T_W (°C)	P_A (mm)	E/PE (%)	GDD5 (degr. days)
<i>Salix</i>	U	15						350
	U	40	−16.0	15.0	−35.0	4.0	3.0	21.0
<i>Sciadopitys</i> #	C	0.5	5.0	15.0	−5.0	5.0	15.0	25.0
<i>Sequoiadendron</i> #	C	5	5.0	20.0	−5.0	11.0	9.0	30.0
<i>Sequoia sempervirens</i> #	W	10	15.0	18.0	5.0	15.0	10.0	25.0
<i>Symplocos</i> #	W	0.5	10.0	25.0	0.0	15.0	20.0	35.0
<i>Tamarix</i>	W	2	12.0	20.0	2.0		22.0	27.0
<i>Taxodium distichum</i> #	W	10	16.0	25.0	5.0	20.0	25.0	30.0
<i>Taxus</i>	C	1	8.0	11.0	0.0	6.0	15.0	20.0
<i>Thalictrum</i>	C	0.5		5.0	−5.0		14.0	
<i>Tilia</i>	U	2	−4.0	16.0	−20.0	7.0	9.0	27.0
	U	10	4.0	15.0	−15.0	7.0	17.0	27.0
<i>Tsuga</i> #	C	0.5	0.0	12.0	−10.0	6.0	5.0	15.0
<i>Ulmus</i>	U	2	−3.0	22.0	−20.0	15.0	7.0	30.0
	U	8	4.0	17.0	−14.0	5.0	15.0	27.0
<i>Vitis</i>	W	0.5	10.0	25.0	−3.0	15.0	18.0	30.0
	W	1	12.0	25.0	0.0	15.0	20.0	30.0
<i>Zizyphus</i>	W	0.3	14.0	25.0	5.0		24.0	29.0

Taxa for which climatic ranges are defined by reference to climatic atlas are marked by the symbol #.

present-day geographic distributions and comparing these to modern climatic data found in climatic atlases (Fauquette et al., 1998a). These data were then integrated in the climatic amplitude table (Table 1, taxa marked by the symbol #). A few of these (*Tsuga*, *Sciadopitys*, *Sequoiadendron giganteum*) were included in the cold taxon group because they certainly belong to mountainous vegetation. The

others were placed in the warm group because they likely originate from low and middle-low altitudinal belts (Fauquette et al., 1998a).

For the E/PE parameter, the values were estimated according to the vegetation type (Prentice et al., 1992). For example, for taxa such as *Calligonum* or *Lygeum*, E/PE was estimated to fall in the 18 and 64% range characteristic of xeric (but not desertic)

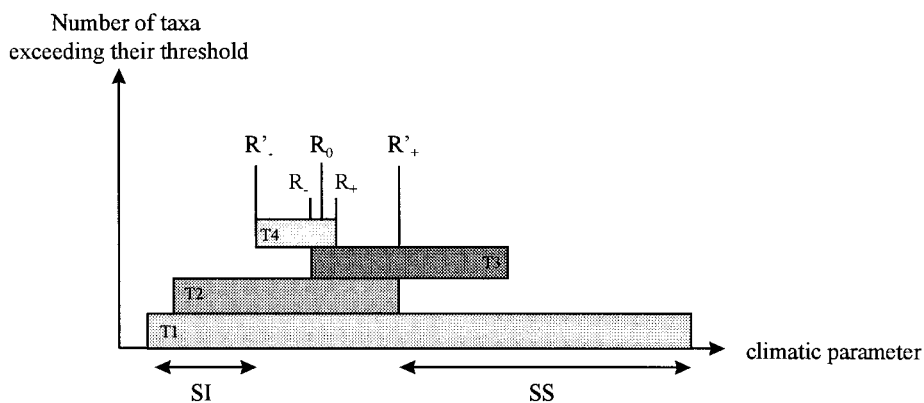


Fig. 2. Example of a composite histogram of some taxa exceeding their presence threshold (T_1 , T_2 , T_3 , T_4) in a pollen spectrum: selection of the most probable climatic range [R_- ; R_+]. When this interval is too small, and thus not so probable, the limits are extended to the next smaller interval [R'_- ; R'_+]. The 'most likely value' (R_0) corresponds to a weighted mean as a function of the inverse of the external surface of the histogram (SI below R_- (or R'_-) and SS above R_+ (or R'_+)). R_0 is constrained to be included in the restricted interval [R_- ; R_+].

environments, whereas for subtropical taxa (such as *Engelhardia*, *Symplocos*, *Distylium* etc.) which grow in moist forest environments, E/PE was estimated at 66 to 100%.

No data were available for the GDD5 parameter for the marker-taxa (this parameter is not given in climatic atlases), so we used multiple regression to calculate the modern relationships among GDD5, mean annual temperature (T_A), mean temperature of the coldest month (T_C) and mean temperature of the warmest month (T_W). This regression analysis was calibrated on the climatic data available for the modern spectra described above, but was restricted to the spectra with T_C higher than 0°C. The resultant relationship was: $GDD5 = 102T_C + 114T_W + 140T_A - 1745$, with r^2 of 0.98.

Another difficulty was to define a significance threshold for the pollen percentages of each marker taxon. For taxa such as *Taxodium* type or *Sequoia sempervirens* type, we used a threshold of 10% because they have a prolific pollen production and, at least for *Sequoia sempervirens*, high percentages indicate the presence of a coastal redwood forest, such as those in California (Heusser, 1983, 1988). Moreover, tests with lower percentages proved that the results were not really sensitive to lower thresholds. For *Engelhardia* (Juglandaceae), of which fossil pollen percentages reach relatively high values, the threshold was placed at 5%. In fact, as the pollen percentages are above 5% in most of the pollen spectra of the sequence, if the threshold was lower than this value, *Engelhardia* would always exceed its threshold, even if pollen percentages were diminishing. This would mask the climatic variations, although variations of the percentages of this taxa are a good climatic signal. As the other subtropical taxa show only a few pollen grains in the Pliocene spectra, their threshold was set to 0.5%.

The climatic amplitudes defined for each marker-taxon were often very large for two main reasons: (1) the pollen grains are usually identifiable only at the genus level, and we were obliged to define climatic amplitudes including all the species of a genus; and (2) in the modern world, plants exhibited large variations according to substratum, exposure, etc.

We must also be aware that modern genera, although closely related to their antecedents, may now

live under slightly different ecological and climatic conditions. For example, some taxa are today restricted to relict areas due to human activities, and thus their modern ranges may not necessarily reflect the climatic requirements of the respective fossil taxa. However, ecological and climatic homologies between Pliocene and modern taxa are usually accepted (Zagwijn, 1960; Pons, 1964), in particular because palynologists work often on the genus level of determination (species were not necessarily the same as today (Roiron, 1992) contrary to genus).

2.3. Test on modern spectra

The method was tested on 886 independent modern pollen spectra obtained from Peyron et al. (1998) which contain many Mediterranean taxa and thus represent the region of our analysis. The quality of the method was assessed by the correlation between observed and estimated parameters for the 886 spectra and by the root-mean-square-error of prediction. For each spectrum and for each parameter we reconstructed two estimates of the climatic conditions: one based on the cold and ubiquitous plants and the other one based on warm and ubiquitous plants. The selection of the final interval was based on a biome assignment proposed by Prentice et al. (1996) and Peyron et al. (1998). When the biome assigned was a cold or cool variety (cold steppe, taiga, tundra, cold deciduous forest, cool conifer forest, cold mixed forest), the cold interval was chosen and when it was a warmer variety (warm steppe, xerophytic woods/shrubs, warm mixed forest, temperate deciduous forest, cool mixed forest), the warm interval was selected.

A first test was made using exactly the same calculation described above, i.e. a weighted mean. But correlation coefficients were poor, especially for P_A , T_W , E/PE and GDD5 (Table 2).

So, a second test was made calculating the 'most likely value' as a simple mean: $R_0 = (R_- + R_+)/2$. For R_0 , the correlation coefficients were a little bit higher than in the first test (Table 3). With the simple mean, they were acceptable for T_A , T_C , T_W , E/PE and GDD5 which were higher than 0.60. The correlation results were poor for annual precipitation in the two cases. However, if the observed values are compared to the estimated climatic ranges (Ta-

Table 2

Correlation coefficients between the observed and estimated climatic parameters, the most likely value corresponding to a weighted mean

Climatic parameters	Coefficients of correlation between observations and estimations
T_A	0.80
T_C	0.75
T_W	0.53
P_A	0.40
E/PE	0.52
GDD5	0.40

ble 3), acceptable results are obtained, even for the annual precipitation (71% of the modern spectra are included in the estimated likely intervals). Note that the correlation was better for the annual precipitation under 1100 mm than above 1100 mm. But for the subtropical Pliocene spectra, this problem is solved because the subtropical taxa give a more precise climatic range and moreover, the weighted mean provides a greater importance to these taxa. In any case, it is generally difficult to reconstruct the annual precipitation on the basis of the vegetation because soil moisture is more important than rainfall amounts. We must thus consider the lower limit as a minimum value which is more reliable than the upper limit. The root-mean-square-errors were relatively poor for T_C , P_A and GDD5 but these errors must be considered in regard to the large inter-annual

Table 3

Correlation coefficients between the observed and estimated climatic parameters, the most likely value corresponding to a simple mean, root-mean-square-error and percentages of spectra included in the climate amplitudes estimated

Climatic parameters	Coefficients of correlation between observations and estimations	Root-mean-square-error	Spectra included in the estimated interval (%)
T_A	0.9	3.1°C	80
T_C	0.88	5.22°C	80.6
T_W	0.67	2.9°C	81.5
P_A	0.52	248 mm	71
$P_A < 1100$	0.52	200 mm	78
$P_A > 1100$	0.26	443 mm	28
E/PE	0.62	15.2%	70
GDD5	0.72	1776°days	50

variability which can be tolerated by the plants, but which is not reflected by the mean climate.

A third test of the method has been realised on the modern spectra, excluding *Pinus* pollen grains of the pollen sum. Indeed, as most of the Pliocene pollen sequences correspond to marine (littoral) sequences, it was necessary to exclude *Pinus* pollen grains of the pollen sum because it is always over-represented in marine coastal sediments due to its prolific production, its good preservation and over-abundance in air and water transport (Suc and Drivaliari, 1991; Calleja et al., 1993; Cambon et al., 1997). If *Pinus* was included in the pollen sum, its over-representation would limit the possible expression of the relative variations of the other taxa (Combourieu-Nebout, 1987). Moreover, the pollen grains of *Pinus* can generally only be identified to the genus level, and the genus *Pinus* has a very large ecological amplitude.

But, as *Pinus* was included in the pollen sum of the modern spectra, it was important to show that its exclusion from the Pliocene pollen spectra had no effect on the results of the climatic estimations. Pollen percentages of the 886 modern spectra have here been calculated without *Pinus*. Correlation coefficients between the observed and estimated climatic parameters and the root-mean-square-error (Table 4) are very similar to the previous ones (Table 3), only the correlation for P_A is a little lower. These results allow us to apply our method to spectra from which *Pinus* is excluded.

For the modern spectra, the ‘most likely value’

Table 4

Correlation coefficients between the observed and estimated climatic parameters when *Pinus* is excluded from the pollen sum, root-mean-square-error and percentages of spectra included in the climate amplitudes estimated

Climatic parameters	Coefficients of correlation between observations and estimations	Root-mean-square-error	Spectra included in the estimated interval (%)
T_A	0.87	3.4°C	78.4
T_C	0.86	5.5°C	76
T_W	0.68	2.9°C	80
P_A	0.45	257mm	68.6
E/PE	0.61	15.8%	66.4
GDD5	0.48	1761°days	48.2

was calculated by a different way than those calculated for the fossil spectra. For the Pliocene spectra, the weighted mean provided a greater importance to subtropical taxa. For the modern ones, this characteristic was not relevant and we thus preferred the simple mean. But anyway, if the two methods did not give exactly the same estimated values, they give the same tendency. For example, we arranged a few modern spectra from regions characterised by different climates, as in a fossil sequence, mimicking typical temporal climatic variations. Six spectra have been chosen: two from Andalusia, another from Sweden, one from southern Turkey and two from Yakoutia. The comparison of the tendency obtained with the two ways of calculation shows that the values obtained are not exactly the same and are different from the observed values but shows clearly that the two ways give the same tendency as the observed one (Fig. 3).

2.4. Test on a modern marine core

We examined the applicability of this method not only for terrestrial modern spectra (discussed above), but also to coastal marine spectra (which represent the greatest number of Pliocene sites) by applying the method to a sub-modern sequence: core KTR05 from the mouth of Grand Rhône River in the northwestern Mediterranean Sea (Cambon et al., 1997), which corresponds to a prodeltaic sedimentation similar to that of the Pliocene sequences.

This borehole (43°18'28"N, 4°51'01"E, water depth 40 m) provides a 7.38-m-long sedimentary sequence, of which the upper 2 m has been studied. The latter interval covers a period of about 6 years from 1985 to 1991, dated by ^{137}Cs , by the evidence of seasonal pollen variations, and by comparison between the quantity of black particles and the intensity of summer forest fires in this region (Suc

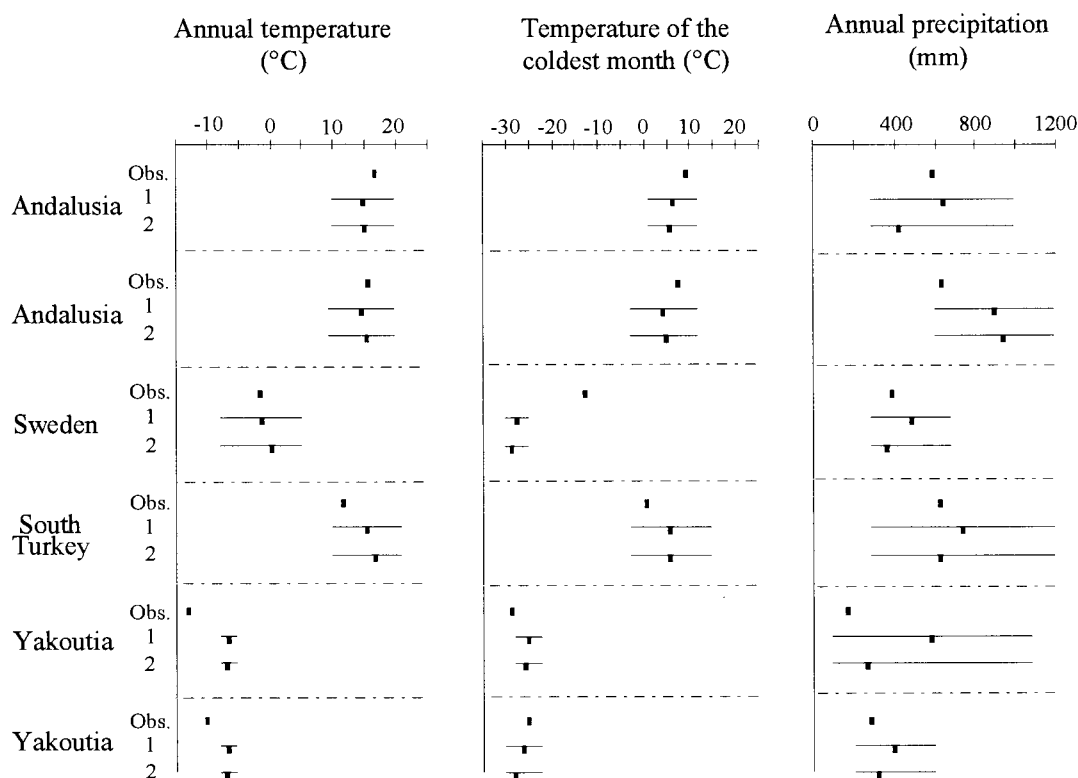


Fig. 3. Six modern pollen spectra, coming from regions characterised by different climates, have been chosen, mimicking typical temporal climatic variations. The spectra come from Andalusia, Sweden, southern Turkey and Yakoutia. The comparison of the tendency obtained with the two ways of calculation (1: simple mean, 2: weighted mean) shows that the inferred values are not exactly the same and are different from the observed values (Obs.) but show clearly that the two calculations give the same tendency as the observed one.

Table 5

Climatic reconstruction for KTR05 core, which corresponds to a prodeltaic sedimentation such as that of the Pliocene sequences, and comparison with observed values

Climatic parameters	R_-	R_0	R_+	Modern values
T_A (°C)	9.5	14.1	18.8	13.7
T_C (°C)	−3.3	3	9.4	6.5
T_W (°C)	19.8	24.8	29.8	21.4
P_A (mm)	594	933	1273	686
E/PE (%)		no result		71
GDD5 (°C)	1973	3055	4136	3200

No estimate has been obtained for E/PE due to the lack of enough taxa exceeding their presence threshold for this parameter.

et al., in prep.). We estimated the modern climate from a single spectrum representing the average of all samples in the sequence, which was comparable to modern surface spectra which cover a more or less long time span. The use of this average value also reduces the effects of seasonal variation on the outcome of the analysis. The most likely value calculated corresponds to a simple mean as for modern surface spectra.

Table 5 provides the comparisons of our estimates of the climate with the observed values for this region. The modern values encompassed the estimated climatic ranges [R_- ; R_+]. For annual temperature and GDD5, the estimated most likely values (R_0) were close to the modern values. However, the correlation was poorer for the other parameters, and it was not possible to estimate E/PE as there were not enough taxa exceeding their threshold for this parameter. The overall results indicate that it is possible to apply this technique to marine cores with a good degree of reliability, at least for some climatic parameters.

3. Application to a Pliocene sequence: Garraf 1

3.1. Location of the site

The Garraf 1 borehole (Suc and Cravatte, 1982) is situated along the Mediterranean shore in Catalonia (Spain), near the southern edge of the mouth of the Llobregat River. The core was collected a few kilo-

metres southeast of Barcelona (41°10'N, 2°01'E), on the continental shelf. The borehole penetrated post-Miocene sediments which represent deltaic filling of the ancient mouth of the Llobregat River. The geomorphology of this site was established by a strong erosion, that lead to the Llobregat canyon-cutting, during the Messinian salinity crisis, then followed by infilling during the subsequent Zanclean period of high sea level (Clauzon et al., 1990). The sedimentary record from the borehole consists of a 875 m thick sequence composed of grey clays (1300 to 1228 m), sand (1228 to 1160 m), and grey to green clays (1160 to 425 m). Pollen analysis was conducted on 47 samples which cover the end of the Miocene and almost the entire Pliocene, and, although these samples are from borehole cuttings rather than continuous sediment cores, the pollen samples provide a good coverage for this period.

3.2. Synthetic pollen diagram and palaeoclimatic reconstructions

The Garraf 1 sequence (Fig. 4) was dated by biostratigraphy using a comparison of the borehole foraminifera (Suc and Cravatte, 1982) and nannoplankton (Matias i Sendra, 1990) records to the Mediterranean standard biozonations (foraminifers: Cita, 1975; nannoplankton: Rio et al., 1990) (Fig. 5). Moreover, climatostratigraphic correlations were established between the northern European Pliocene and Mediterranean Pliocene (Suc and Zagwijn, 1983).

The four lowermost pollen spectra (1300 to 1228 m) in the Garraf 1 diagram are dated Late Miocene and were probably deposited before the Messinian salinity crisis. These spectra are dominated by Taxodiaceae, *Engelhardia* and Poaceae, and have significant levels of Asteraceae (including *Artemisia*) and *Ephedra* pollen. During the early Zanclean (pollen zone PIa: 1210 to 1090 m), the pollen spectra are characterised by the dominance of subtropical trees (*Taxodium* type, *Engelhardia*, and others), suggesting the presence of coastal forest and *Taxodium*-type swamp environments. In contrast, the second Zanclean phase (pollen zone PIb: 1090 to 910 m) is characterised by a decrease in pollen of subtropical trees and an increase in *Tsuga*, *Carpinus*, Asteraceae, Poaceae, *Artemisia* and *Ephedra* pollen, which indicates drier conditions than earlier. Follow-

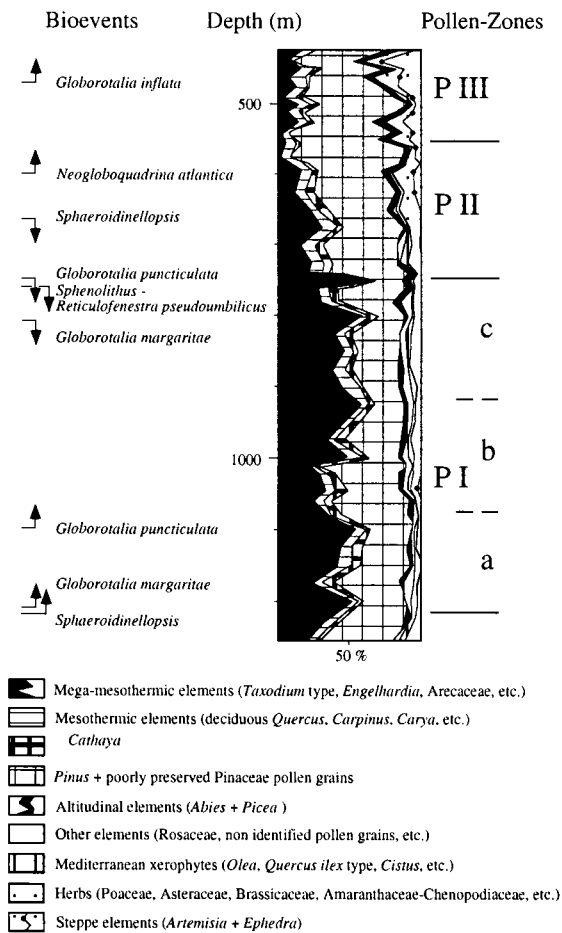


Fig. 4. Synthetic pollen diagram of the Garraf 1 borehole.

ing this, a major increase in *Taxodiaceae* marks a third phase (pollen zone PIc: 910 to 745 m), reflecting a return to moist environments. Suc and Zagwijn (1983) demonstrated the correlation of the three subdivisions pollen zone PI with those of the Brunsumian in northwest Europe.

Subtropical trees (*Taxodiaceae*, *Engelhardia* and *Myrica*) were no longer dominant during the early Piacenzan (pollen zone PII: 745 to 555 m) as their pollen percentages decreased as those of deciduous warm-temperate elements, herbs, and Mediterranean xerophytes increased. This marks a cooler period than the previous one. It corresponds to the Reuverian period in northwest Europe (Suc and Zagwijn, 1983). The youngest period represented in the Garraf 1 borehole (pollen zone PIII: 555 to 425 m) is

characterised by a major decrease in *Taxodiaceae* pollen, whereas pollen of *Asteraceae* (*Artemisia* in particular), *Poaceae*, *Cupressaceae*, and *Ephedra* increased. This pollen zone represents the first large-scale cooling of the late Cenozoic in the Northern Hemisphere, i.e. the Pretiglian (Suc and Zagwijn, 1983).

The climatic estimate was calculated for each pollen spectrum of the Garraf 1 sequence. As described in a previous section concerning the test of the method, the pollen of *Pinus* was excluded from the pollen sum, as the pollen of *Pinus* is over-represented in marine coastal sediments (Calleja et al., 1993; Cambon et al., 1997; Suc and Drivaliari, 1991).

As the borehole deposits consist of marine coastal sediments, the pollen spectra represent the integration of many vegetation belts across the elevational gradient. However, the method used here allowed us to separate the low/middle-low altitude vegetation belt and that from middle-high/high elevations, and thus we could estimate palaeoclimatic conditions for the coastal belt. As only the taxa that exceed their thresholds (presence/absence and/or abundance) are used in the climatic reconstruction of a given pollen spectrum, only a few taxa from each assemblage are taken into account (Fig. 6). A few other taxa are occasionally significant, and the palaeoclimatic estimates are shown in Fig. 7.

4. Discussion

The Garraf 1 pollen diagram is particularly important because it is a continuous well-dated long record that provides a clear palaeoclimatic record from the lowermost Zanclean (5.32 Ma) to the latest Gelasian (about 1.8 Ma). The changes interpreted from this record are as follows.

In the northwestern Mediterranean region, the Early Pliocene was warm and humid, with a trend toward progressively cooler and drier conditions through time, from the beginning to the end of the sequence. At around 4.5 Ma, a cooling is seen in the pollen data, marked by a decrease in thermophilous trees and an increase in herbs. Our quantitative reconstruction does not indicate changes through this period. In fact, the decrease in subtropical plants was not very important and even though their pollen

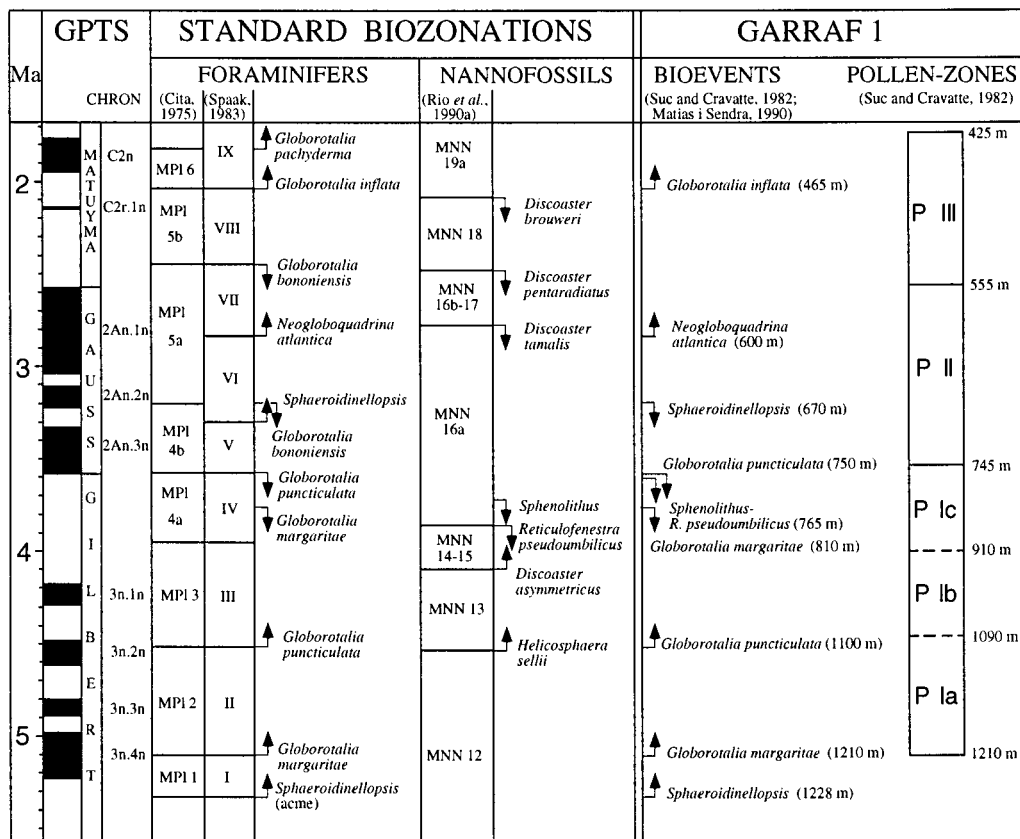


Fig. 5. Bioevents and pollen-zones of the Garraf 1 sequence and the Mediterranean Pliocene standard chronostratigraphy. (Data from Cita, 1975; Suc and Cravatte, 1982; Spaak, 1983; Matias i Sendra, 1990; Rio et al., 1990.)

percentages decreased, they still exceeded the thresholds and we conclude that the climate did not change significantly during this interval.

This cooling was followed by a warm period during which the temperatures were higher than today. Annual precipitation was also very high, falling between 1100 and 1600 mm (versus ~610 mm today). For the parameter E/PE (ratio of actual evapotranspiration to potential evapotranspiration), the reconstructed high values (65 or even 80 to 100%) from this time leads us to think that forest was present on the coast, an interpretation that is confirmed by the high percentages of arboreal pollen (in particular those of the *Taxodium* type). The values of GDD5 (growing degree-days above 5°C) were high, between 43,800 and 5000–5500° days.

Another cooling occurred at around 3.6 Ma, immediately after the Zanclean–Piacenzian boundary

(Suc and Zagwijn, 1983; Suc, 1984). This event was characterized at Garraf 1 by a strong decrease in the pollen of subtropical trees and by an increase in herb pollen. This event is evident in the palaeoclimatic reconstruction, even though the decrease of the annual temperatures was not very pronounced. Indeed, the pollen percentages of subtropical trees continued to exceed their thresholds and thus temperatures must still have been quite high. Nevertheless, the pollen data suggest that the temperature of the warmest month decreased clearly at this time and that E/PE values were less than during the previous period (65 to 100% instead of 80 to 100%). The inferred changes in temperature and moisture were probably responsible for the reduction in the cover of *Taxodiaceae* swamps, the increase in open vegetation, and other changes in vegetation structure (Suc and Cravatte, 1982).

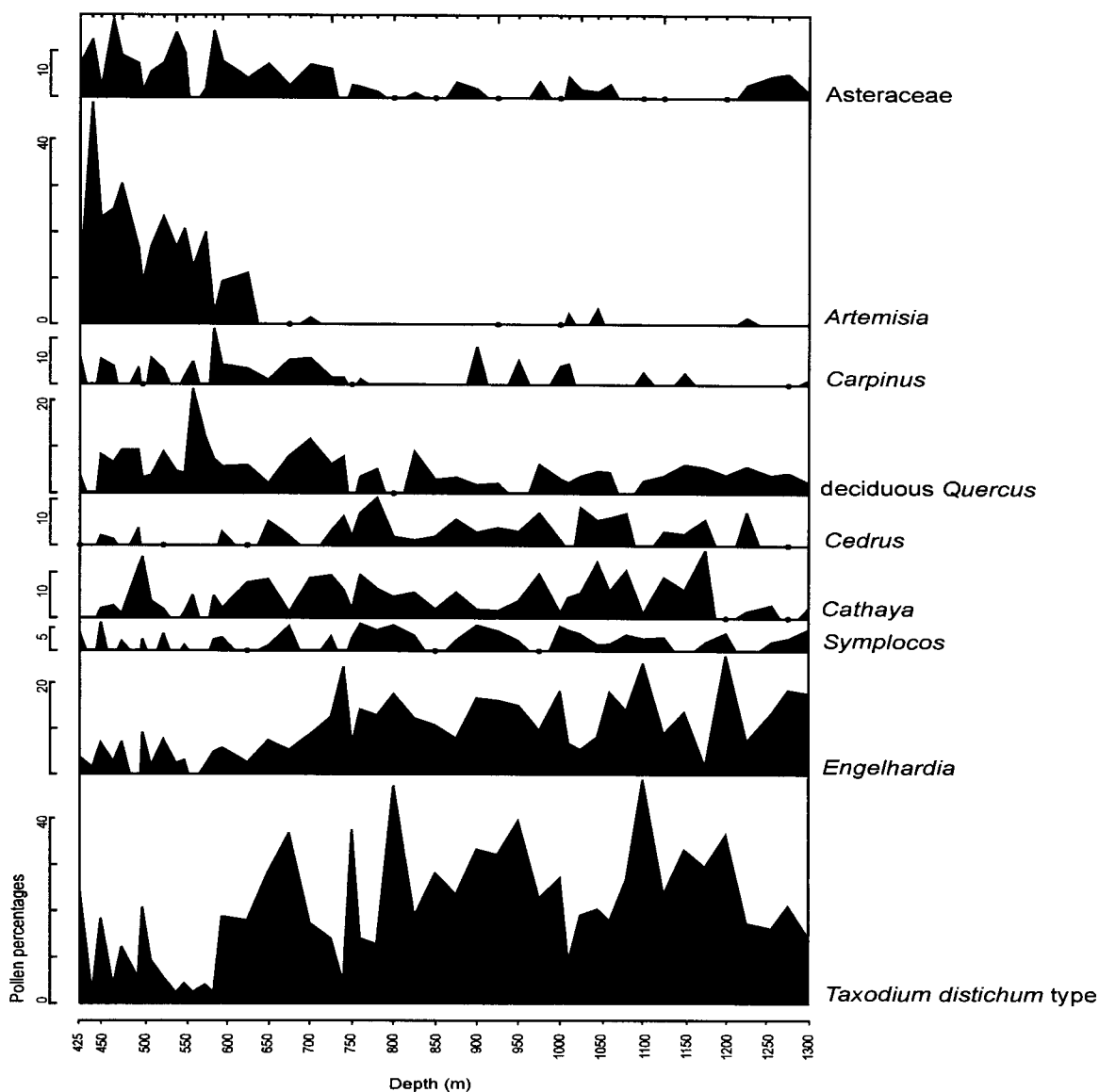


Fig. 6. Curves corresponding to the pollen percentage variations of main taxa which permit inferences of the past climatic parameters at Garraf.

Subtropical taxa progressively diminished between ~ 3.6 and ~ 2.8 Ma, although there were a few oscillations. The last warming period within this interval occurred at around 3.1–3.0 Ma, as illustrated by the occurrence of the final significant percentages of subtropical pollen taxa. This climatic event is not really obvious in the climatic reconstruction. At this time temperature of the warmest month in-

creased (26 to 28°C), although neither the annual temperatures nor the coldest month changed. E/PE was high again (80–100%), as was GDD5 (3800 to 5000–5600 degree-days).

From about 2.8 Ma to the end of the sequence, the pollen diagram is characterized by rapid alternations between steppe and forest linked to glacial–interglacial fluctuations (Suc and Zagwijn, 1983).

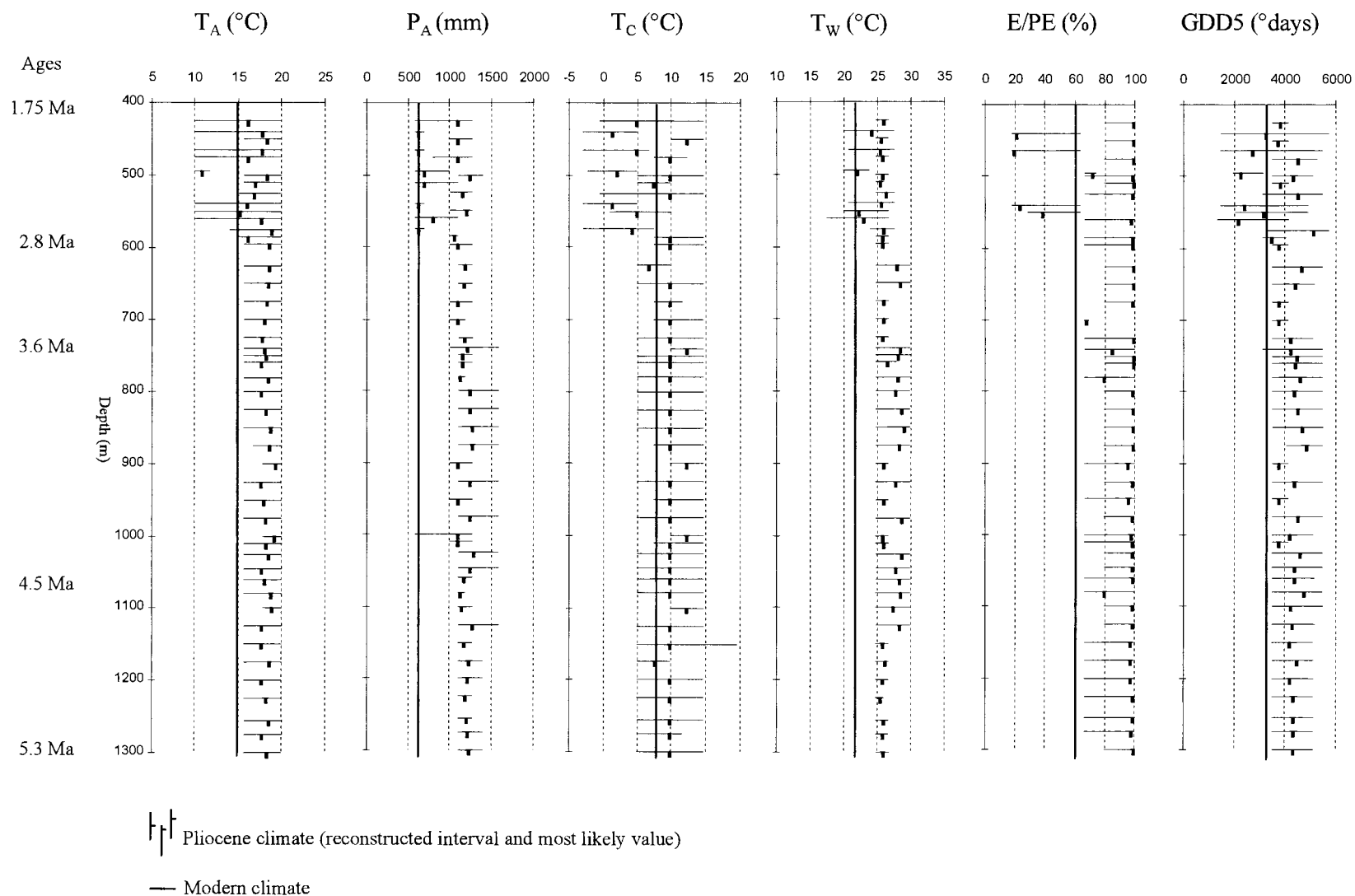


Fig. 7. Climatic estimates for the Pliocene in the northwest Mediterranean according to the pollen content of the Garraf 1 sequence.

These alternations are well marked in our climatic reconstruction: during glacial phases annual temperatures decreased to values similar to those of the present time; during interglacial phases temperatures again increased. Variations in annual precipitation were seemingly rapid through this period and reached very low values during this interval (equivalent to modern ones). Important variations also occurred in other climatic parameters, suggesting rapid climatic changes. However, our method demonstrates that it is not possible to infer lower temperatures from slight decreased relative abundances of subtropical pollen taxa.

Thus, during the Pliocene, before the first high-amplitude glacial/interglacial cycles, our method suggests that annual temperatures were 1 to 5°C warmer, and annual precipitation was 400 to 1000 mm higher, than at present. This interpretation is in agreement with the climates inferred from pollen data by Willard (1994) for a mid-latitude site (36°N) in southeastern Virginia (USA) where annual temperatures were 2.5°C higher than today.

Climatic reconstructions for the Pliocene have also been carried out based on fossil mammal data (Montuire, 1994, 1996; Michaux et al., 1996; Aguilar et al., 1998). Mammalian palaeofaunas suggest warm conditions during the first half of the Pliocene, with the highest mean annual temperatures and precipitation (21°C and 1100 mm, respectively) reached between 4 and 3 Ma. These data also indicate that mean annual temperature declined to 13°C and mean annual precipitation to 700 mm with the onset of the Late Pliocene glacial–interglacial cycles. These estimates are very similar to those we obtained from the Garraf 1 pollen data, although there are some differences. For example, a cooling is evident in both data sets at approximately 4.5 Ma but appears to be of larger magnitude in the analysis of the mammalian data. However, this method does not provide confidence intervals for the estimates, and, in any case both methods record the same broad-scale changes and similar palaeoclimatic estimates.

Our results are also in agreement with Sea Surface Temperature (SST) estimates based on dinoflagellate cysts (Edwards et al., 1991), planktonic foraminifera (Dowsett and Poore, 1991), and marine ostracodes (Cronin, 1991; Cronin et al., 1993). These data suggest that at about 3 Ma both winter and sum-

mer SST's in the north were a few degrees Celsius warmer than at present.

Mediterranean $\delta^{18}\text{O}$ curves based both on planktic (Thunell et al., 1990) and benthic (Vergnaud Grazzini et al., 1990) foraminifera show a cooling trend from the Early Pliocene to the Early Pleistocene, with an accelerated rate of change after 3.1 Ma. The major palaeoclimatic variations estimated from our pollen data are consistent with those shown by the $\delta^{18}\text{O}$ curves in this region. $\delta^{18}\text{O}$ data from benthic foraminifers of the North Atlantic Ocean (Tiedemann et al., 1994) show the same trends as the Mediterranean records, with a progressive cooling through the Pliocene accelerating after approximately 3.2 Ma.

Pliocene palaeoclimatic reconstructions provide information for the evaluation of how well atmospheric general circulation models (ACGM's) can simulate warmer-than-modern global climates (Crowley, 1991). In a Pliocene simulation using the Goddard Institute for Space Sciences (GISS; Chandler et al., 1994) ACGM, temperature estimates for Catalonia are similar to those obtained from our analysis of the Garraf 1 record, with a simulated increase in mean annual temperature increase of 4°C.

This new method has been developed to reconstruct the climate of relatively ancient periods for which no modern palynological or vegetational analogues are available, but it can be easily applied to more recent periods, such as the last glacial–interglacial cycle (Fauquette et al., 1998b). Results obtained for this period are consistent with the numerous climatic reconstructions made, for example, from pollen data with the best analogues method (Guiot et al., 1992) or from foraminifers (Cortijo et al., 1994).

5. Conclusions

We present the first quantitative climatic reconstruction of the entire Pliocene for the northwestern Mediterranean region using a new method that allows us to produce climatic estimates for pollen spectra which have no modern analogues. This method is based on determining the overlap in the modern climatic amplitudes of individual taxa present in the fossil pollen spectrum.

Most Pliocene deposits were deposited in shallow coastal marine environments. Our new method is applicable to coastal marine pollen assemblages, as we have demonstrated by estimating modern climatic parameters from modern deposits that are analogous to the Pliocene sediments. The application of our new method appears to give results that are comparable to previous qualitative interpretations of Pliocene pollen diagrams from the Mediterranean region and Europe (Zagwijn, 1960; Bertini, 1994; Suc et al., 1995a,b). During the Early Pliocene mean annual temperatures were 1 to 5°C higher than those of today and mean annual precipitation was 400 to 1000 mm higher. These results are also in agreement with estimates based on European mammals; marine ostracodes and planktic foraminifers from the North Atlantic and the Mediterranean; and North American pollen data. Now that our new method has been established for one Pliocene site, it can be applied to other pollen profiles in Mediterranean regions to allow inter-regional comparisons and to provide the basis for palaeoclimatic maps.

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Climate and biomes in the West Mediterranean area during the Pliocene

Séverine Fauquette ^{a,*}, Jean-Pierre Suc ^b, Joël Guiot ^a, Filomena Diniz ^c, Najat Feddi ^d,
Zhuo Zheng ^e, Ezzedine Bessais ^{f,1}, Androniki Drivaliari ^g

^a Institut Méditerranéen d'Ecologie et de Paléoécologie, UPRESA CNRS 6116, Case 451, Faculté de Saint-Jérôme,
13397 Marseille cédex 20, France

^b Centre de Paléontologie stratigraphique et Paléoécologie, UMR CNRS 5565, Université Claude Bernard Lyon I,
69622 Villeurbanne cédex, France

^c Departamento de Geologia, Universidade de Lisboa, 1294 Lisbon codex, Portugal

^d Département de Géologie, Faculté des Sciences 'Semailia', Université de Cadi Ayyad, Boulevard Prince Moulay Abdellah,
B.P. S 15, Marrakech, Morocco

^e Faculty of Geology, Zhongshan University, 510275 Guangzhou, China

^f Laboratoire de Palynologie, Institut des Sciences de l'Evolution, Université des Sciences et Techniques du Languedoc,
34000 Montpellier, France

^g Centro de Geologia, 34 P. Karolidou, 54453 Thessaloniki, Greece

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Abstract

A new pollen-derived method of climatic quantification, based on the mutual climatic range of plant taxa, has been applied to 17 Pliocene pollen sequences in the West Mediterranean area. The latitudinal gradient observed in the pollen data was confirmed by the climatic reconstructions: there is a gradient from north to south both for temperatures and precipitation. At the beginning of the Pliocene (5.32–5 Ma), the climate in the North Mediterranean area was, on average, warmer and more humid than today (respectively 1–4°C and 400–700 mm). In the South Mediterranean region, the climate was both warmer and drier than today (respectively equal to or 5°C higher and drier or equal humidity). The pollen-based climate estimates were then used to reconstruct biomes for the region. The results show the occurrence of three biomes: the broad-leaved evergreen/warm mixed forest, the xerophytic woods/scrub biome and the warm grass/shrub biome. These biomes are still represented today in the Mediterranean region despite different thermic and water conditions. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: climatic quantification; biomes; Pliocene; pollen data; West Mediterranean area

1. Introduction

The Pliocene period runs from 5.32 to 1.77 Ma. During this time interval, mid-latitude areas made

the transition from relatively warm climates to the cooler climate of the Pleistocene. This transition, which also saw the emergence of early Man, contains the first glacial–interglacial cycles of the Northern Hemisphere (Leroy et al., 1998). In addition, the reconstruction of Pliocene climate is of prime importance, because the Pliocene is a period during which global average temperature was significantly

* Corresponding author. Tel.: +33-4-9128-8527; Fax: +33-4-9128-8668; E-mail: severine.fauquette@lbhp.u-3mrs.fr

¹ Deceased.

higher than today, and may correspond to the future climate on Earth, resulting from the increasing greenhouse effects (Dowsett and Poore, 1991; Dowsett et al., 1992; Cronin and Dowsett, 1993). The Mediterranean region s.l. is the best disposed area for Pliocene climatic reconstructions (Suc et al., 1995b) because of: (1) its abundance in generally well chronologically calibrated sequences rich in pollen content; (2) the similarity of its paleogeographic features to those of the present-day, characterised by its longitudinal length and the presence of high mountains. These may provide an idea of the climate range through middle to high latitudes.

Since the seventies, Pliocene pollen records from the Mediterranean have been systematically studied using a modern botanical approach. This has allowed reliable vegetation reconstructions to be made (Suc, 1981; Cravatte and Suc, 1981; Suc and Cravatte, 1982; Diniz, 1984a,b; Zheng, 1990; Drivaliari, 1993; Bertini, 1994; Suc et al., 1992, 1995a,b). The lower Pliocene (Zanclean stage) is particularly rich in pollen data for the whole region.

In this paper we present the results of climatic quantification for 17 sites around the West Mediterranean area, firstly for the whole Pliocene, in order to observe temporal climatic variations, then for the period 5.32–5 Ma (the beginning of the Pliocene), to observe spatial climatic variations. From the second set of results, a biome reconstruction has been made for the same period. Finally, our results have been compared with the simulations obtained with the Goddard Institute Space Studies (GISS) general circulation model (Chandler et al., 1994).

2. Methodology

The climatic reconstruction of the Pliocene, based on pollen data, requires a new method of quantification. Methods based on associations of pollen-taxa (e.g. the best analogue method Guiot, 1990) cannot be used due to the presence within the fossil spectra of temperate, warm-temperate and subtropical plants that are no longer found in the Mediterranean region. So, a new climatic amplitude method, modified to take into account taxa abundances, was carried out by Fauquette et al. (1998a,b). This method is briefly described below.

The basis of the technique is the transposition of the climatic requirements of a maximum number of modern taxa to the fossil data. The first phase was to determine, from the literature, the present-day distribution of a few marker-taxa of the Mediterranean Pliocene. These were subtropical plants and some taxa that still exist in the Mediterranean region, which have well defined climatic ranges (Fauquette et al., 1998a).

The second phase was to define the climatic amplitudes of various pollen taxa on the basis of almost 8000 modern pollen spectra. These are surface samples or core-tops originating from Eurasia and North America, gathered by B. Huntley, P.J. Bartlein (pers. commun.) and Peyron et al. (1998). These samples cover a broad range of climate types, from boreal to warm-temperate climates.

In contrast with the best analogue method, this approach does not rely on the analysis of entire pollen assemblages, but on the relationship between the relative pollen abundance of each individual taxon and the climate.

The distribution of pollen percentages in relation to bioclimatic parameters has been analysed for some 60 taxa present in the modern spectra. Thresholds of presence/absence and of abundance were established. Above the presence/absence threshold the taxon is assumed to be present locally, and above the abundance threshold it is considered to have a substantial local presence. If the pollen percentage of a taxon exceeds one of these thresholds, the possible values for the corresponding climatic parameters may be restricted to a precise range. On the other hand, if this percentage is below the presence/absence threshold, the climatic range of the taxon is not taken into account, as the taxon is probably not locally present: pollen percentages below this level may reflect long-distance transport by wind or water.

So, in a given spectrum, each taxon exceeding the presence threshold provides a climatic range. This interval can be defined more accurately by comparison with the climatic ranges of other taxa exceeding their presence threshold. The most probable climate for a set of taxa exceeding their thresholds is therefore provided by the smallest climatic range suitable for a maximum number of taxa. The climatic estimate is given as a climatic range and a 'most likely value'. This value is a mean, weighted to give im-

portance to the subtropical taxa (Fauquette et al., 1998b).

The pollen of *Pinus* and non-identified Pinaceae (due to poor preservation) have been excluded from the pollen sum of the fossil spectra. The pollen grains of *Pinus* are over-represented in marine coastal sediments, due to its prolific production and overabundance in air and water transport (Suc and Drivaliari, 1991; Cambon et al., 1997). Their inclusion in the pollen sum limits the possible expression of the relative variations of the other taxa (Combourieu-Nebout, 1987). Tests made with and without *Pinus* in the pollen sum showed that its exclusion from the pollen sum does not alter the results of climatic estimates (Fauquette et al., 1998b).

As we wish to calculate climatic estimates for low and mid-low altitudes for each Pliocene site, the plants were separated into three groups: ubiquitous plants (U), plants growing in cold conditions (C) (at high altitudes and/or high latitudes) and plants growing in warm conditions (W) (at low altitudes and/or low latitudes) (Fauquette et al., 1998b). The climate at low and mid-low altitudes therefore corresponds to the interval defined by the taxa of group 'W'. For the southern sites (North Africa, southern Spain, and Sicily), some taxa were re-indexed according to the north–south temperature increase. For example, *Cathaya* grew at middle altitude in the North Mediterranean area and Europe, but at higher altitudes in the South Mediterranean area. Therefore, in North Africa and southern Spain, it was assigned to the group 'C'. The change in latitudinal level, then, is compensated by the change in altitudinal level (today, 1° in latitude corresponds to 110 m in altitude; Ozenda, 1989).

For the first part of this study concerning the evolution of the climate in each site through time, three climatic parameters have been estimated: mean annual temperature (T_A), mean annual precipitation (P_A) and available moisture, i.e. the ratio of actual evapotranspiration to potential evapotranspiration (E/PE). For the reconstruction of the climate at 5.32–5 Ma, two other parameters were included: the mean temperature of the coldest month (T_C) and of the warmest month (T_W). As biomes cannot be deduced directly from pollen data because of the lack of vegetation modern analogues, the two last climatic parameters together with the value of the ratio E/PE were used for the biome reconstruction.

3. Application to West Mediterranean pollen sequences

This method has already been applied to a Pliocene pollen sequence, Garraf 1 (Fauquette et al., 1998b). It appears to give reasonable climatic estimates when compared to the interpretation of numerous Pliocene pollen diagrams in the Mediterranean region and elsewhere in Europe (Zagwijn, 1960; Bertini, 1994; Suc et al., 1995a,b). Here, the technique has been applied to other sites in the Mediterranean region.

Based on qualitative and quantitative examination of the pollen diagrams, Suc et al. (1995b) have recognised four vegetational domains during the Pliocene: West Africa, West Europe, Southwest Mediterranean and Northwest Mediterranean.

In this paper, analysis was made on 17 sites (18 sites considering the site of Garraf 1 which has already been studied) (Fig. 1) from three of these vegetational domains.

(1) The Northwest Mediterranean domain: Saint-Martin du Var, La Combe and Saint-Isidore quarries, near Nice, France (Zheng and Cravatte, 1986; Zheng, 1990); Pichegu quarry in the Rhône Ria (Suc, 1981); Cap d'Agde 1 borehole (Suc, 1989) in Languedoc; Perpignan boreholes (Mutualité Agricole and Canet 1; Cravatte et al., 1984); and Vivès, Le Boulou, and Nidolères (Suc, 1976, 1989; Suc et al., 1995a) in Roussillon.

(2) The Southwest Mediterranean domain: Tarragona E2 borehole in Catalonia (Bessais and Cravatte, 1988); Andalucia G1 borehole in southern Spain (Suc et al., 1995b); Habibas 1 borehole (Suc, 1989) and Nador 1 borehole in Morocco (N. Feddi, in prep.); Oued et Tellil in Tunisia (Suc et al., 1995b); and finally Capo Rossello outcrop in Sicily (Suc and Bessais, 1990; Suc et al., 1995a).

(3) For comparisons, a site from the West European domain has been chosen: Rio Maior F16 borehole in southern Portugal (Diniz, 1984a,b).

Most of these sequences have been dated using foraminifera, and/or nannoplankton, magnetostratigraphy, mammal biochronology (Fig. 2). The base of the Pliocene is easily identifiable in all the Mediterranean marine sections. The Pliocene sequences follow the erosional phase corresponding to the deep Mediterranean salinity crisis (Clauzon et al., 1990),

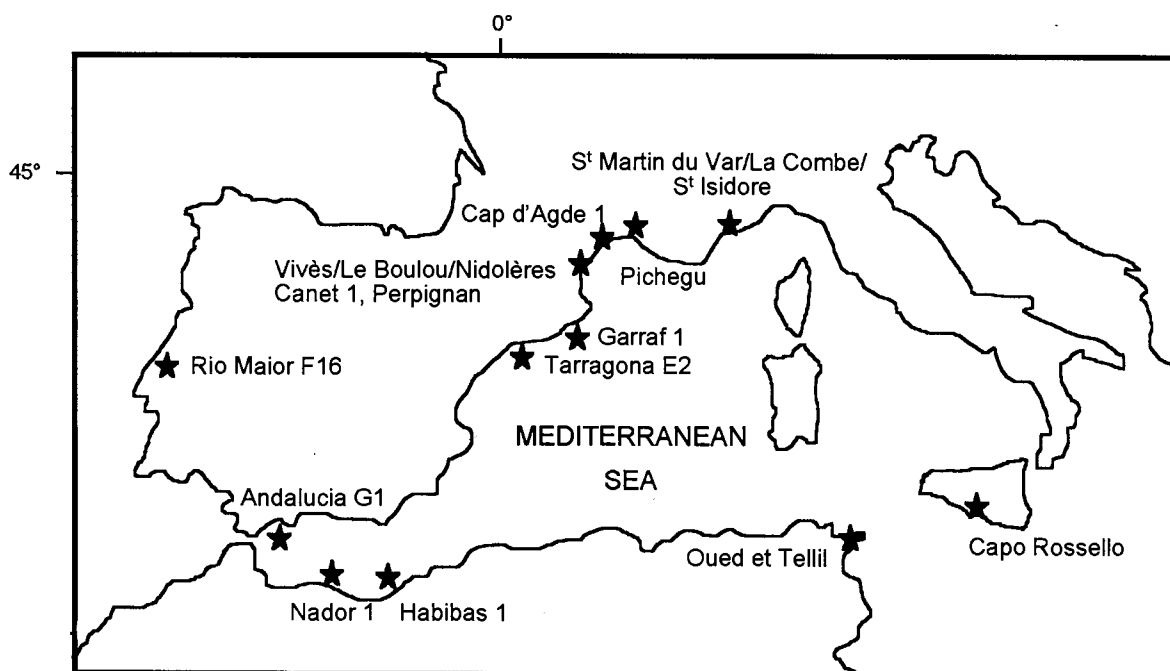


Fig. 1. Location map of the studied Pliocene sites around the West Mediterranean region.

so lower Pliocene sediments overlie the Messinian erosional surface. The sequence of Rio Maior is climatostratigraphically correlated to the synthetic pollen zones of Zagwijn (1960) and Suc (1982) and, therefore to the standard marine biostratigraphy via the Mediterranean pollen diagrams (Suc and Zagwijn, 1983).

Some of these sequences cover the earliest to the latest Pliocene: Rio Maior, Andalucia, Tarragona, Nador and Garraf. The others cover shorter periods, mainly to the lower Pliocene (Fig. 2).

The sediments of the sequences used in this study are derived from diverse sources, but none are deep marine sediments. Comparisons may be made between deltaic, continental or littoral sediments, if the differences in pollen transport are taken into account. For example, fluvial transport is the dominant pollen source for deltaic or marine littoral sediments, as seen in the Rhône River in France (Cambon et al., 1997) or as in California (Heusser, 1988). However, the climatic reconstruction method has been tested on several types of pollen spectra (Fauquette et al., 1998b): modern surface pollen spectra (mosses or core-top) and also on sub-modern coastal marine

spectra (KTR05 core from the Rhône River, France; Cambon et al., 1997). The results obtained are consistent and allow us to apply the method to the diverse Pliocene sites.

4. Pliocene climate in the West Mediterranean area

4.1. Climatic evolution during the Pliocene

4.1.1. Alpes-Maritimes (southern France)

This region is represented by three discontinuous sequences (Saint-Martin du Var, La Combe and Saint-Isidore). These records have allowed the reconstruction of climate from the beginning of the Zanclean to the first part of the Piacenzian (Fig. 3).

Within each pollen sequence, some slight oscillations are recorded for both the annual temperature and the annual precipitation. The ratio E/PE, however, is stable along the sequences. For this region, the climatic estimates indicate that annual temperatures and annual precipitation were higher, approximately 1.5–5°C and 500–900 mm higher than today,

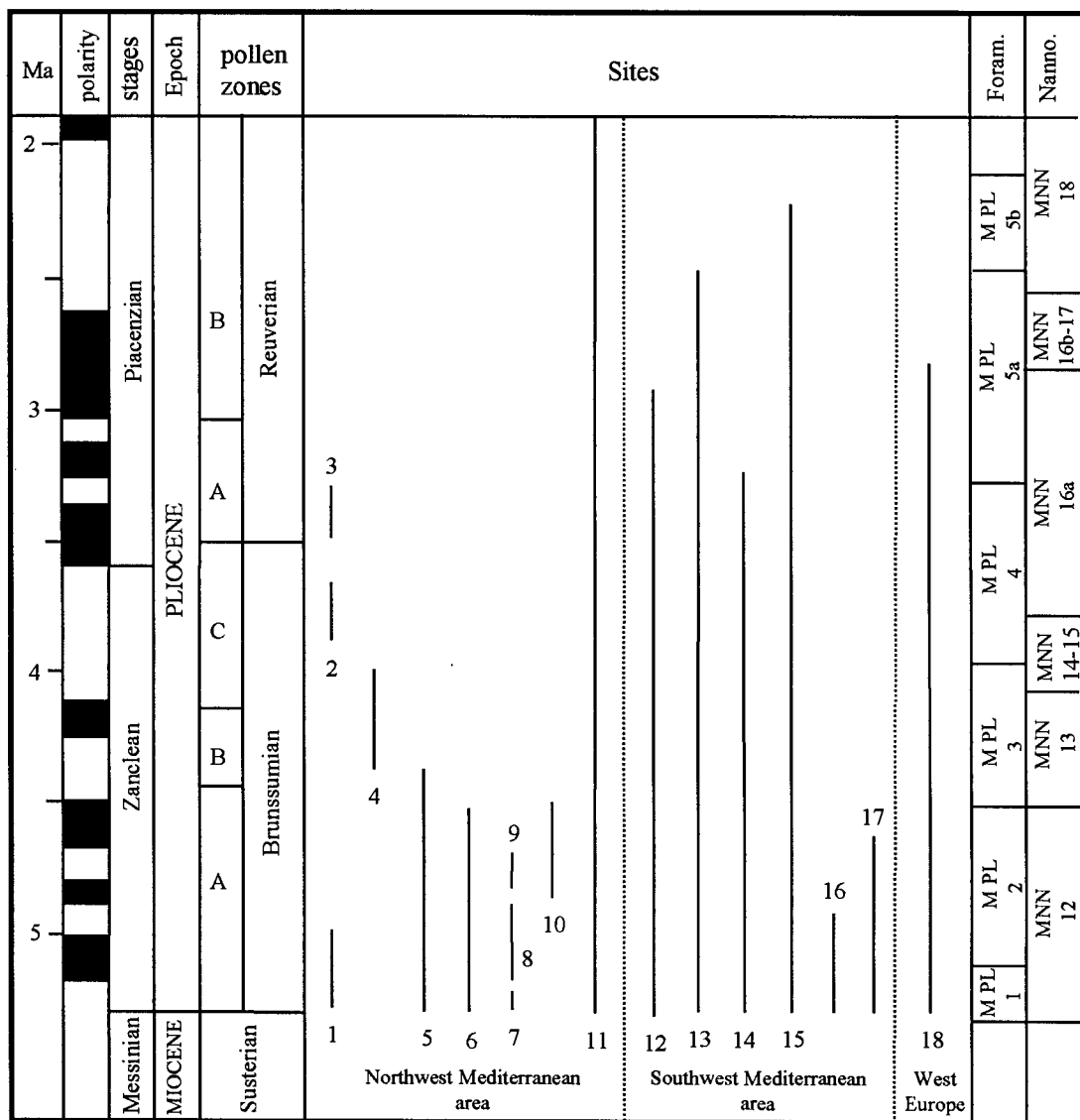


Fig. 2. Chronostratigraphic position of the 18 sites studied. 1 = Saint-Martin du Var; 2 = La Combe; 3 = Saint-Isidore; 4 = Pichegu; 5 = Cap d'Agde 1; 6 = Canet 1; 7 = Vivès; 8 = Le Boulou; 9 = Nidolères; 10 = Perpignan (Mutualité Agricole F1); 11 = Garraf 1; 12 = Tarragona E2; 13 = Andalusia G1; 14 = Habibas 1; 15 = Nador 1; 16 = Oued et Tellil; 17 = Capo Rossello; 18 = Rio Maior F16. Pollen zones according to Zagwijn (1960) and Suc (1982). Foraminifer zones after Cita (1975), nannoplankton zones after Rio et al. (1990).

respectively. The ratio E/PE was also elevated, between 80 and 100% (70% today).

Subtropical trees (especially *Sequoia*-type) decrease from Saint-Martin du Var (earliest Zanclean) to Saint-Isidore (earliest Piacenzian). At Saint-Isidore, mesophilous and herbaceous taxa progressively

replace Taxodiaceae (Zheng, 1990). The variations observed in the pollen spectra represent changes in vegetation. These changes may be attributed to the climatic change which took place at approximately 3.5 Ma (Zagwijn, 1960; Suc, 1982; Dowsett et al., 1992) and is recorded in some localities, in partic-

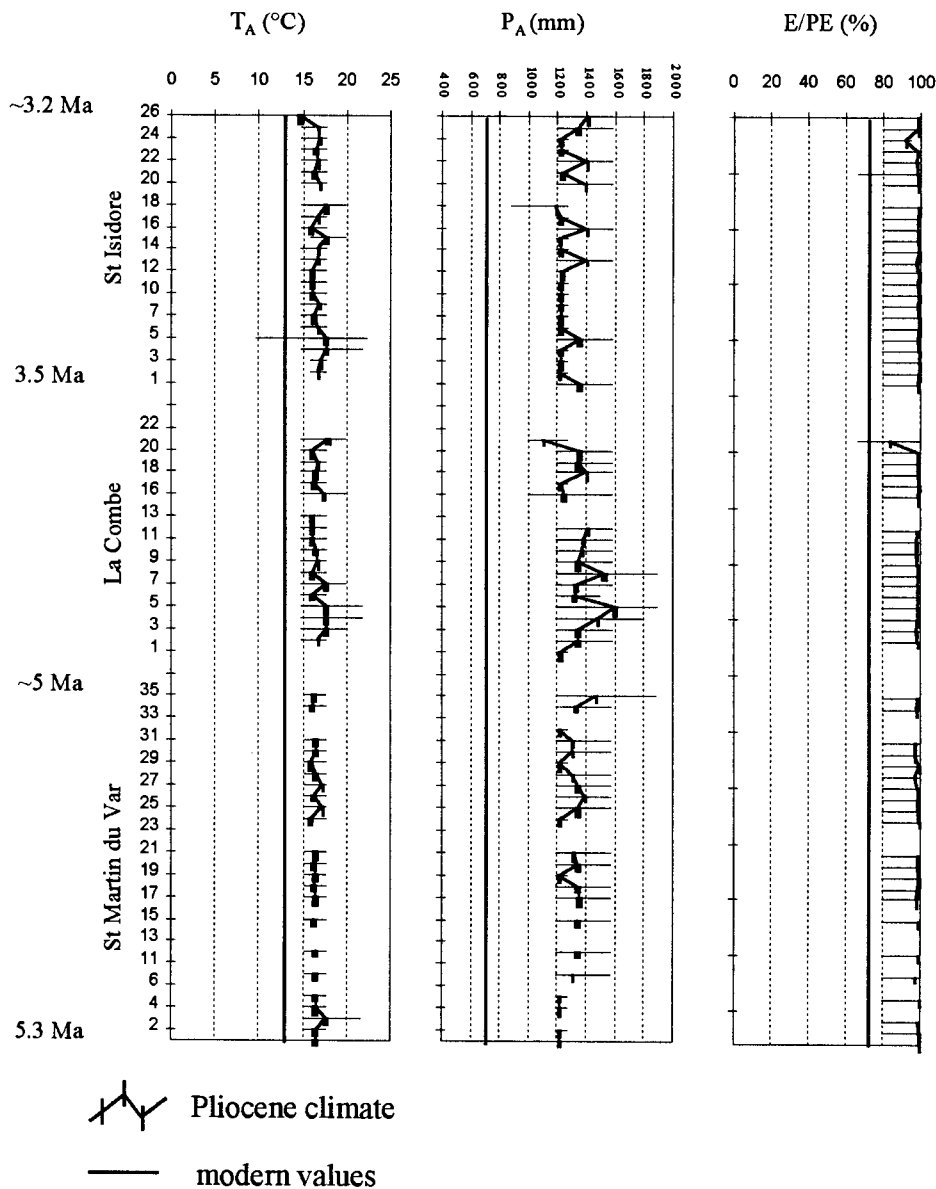


Fig. 3. Climatic evolution in the Alpes-Maritimes (France) during the early Zanclean (Saint-Martin du Var), the late Zanclean (La Combe) and the early Piacenzian (Saint-Isidore).

ular at Garraf 1 (Suc and Cravatte, 1982; Fauquette et al., 1998b) but not in the climatic estimations of Saint-Isidore.

This change may correspond to the appearance of a seasonal thermal regime in the West Mediterranean region, also characterised by a decrease in annual rainfall, more extreme in humid areas (Suc,

1989). In our climatic reconstructions, no decrease in temperatures (annual and also of the coldest month, not presented in this paper) were recorded at Saint-Martin du Var and Saint-Isidore, but a slight decrease in annual precipitation was detected at Saint-Isidore (around 1200 mm versus 1200 to 1600 mm at Saint-Martin du Var and La Combe). No change was

observed in the ratio E/PE, the humidity was, therefore, still sufficient to ensure that the Taxodiaceae forest persisted, albeit with a slight decline.

4.1.2. Rhône (southern France)

The pollen sequence of Pichegu was taken from deltaic sediments sampled in an exposed section of the Rhône Ria (Suc, 1981). It covers a relatively short period, from about 4.3 to 4 Ma. This sequence is dominated by arboreal pollen grains, indicating a forest environment. Taxodiaceae are abundant, particularly in the lower part of the section. In the upper part, corresponding to the transition between the marine clays and the continental deposits, they suddenly decrease, with a corresponding increase in taxa such as *Olea*, *Phillyrea*, *Platanus*, *Vitis* and *Cistus*.

Many pollen spectra do not provide climatic estimates in this sequence (as few taxa exceed their threshold). As a result, the calculation was made based on a single spectrum summed from the whole sequence. Annual temperatures were between 15 and 17.7°C (i.e. 1.6 to 4.2°C higher than today), precipitation and E/PE were similar to those of Saint-Martin du Var (respectively 1200 to 1500 mm and 80 to 100%).

4.1.3. Languedoc (southern France)

This region is represented by the sequence Cap d'Agde 1 (Suc, 1989). Cap d'Agde is included in the same vegetational zone as the sites of Saint-Martin du Var and Pichegu, the Northwest Mediterranean area, but lies to the west. This sequence covers the period between 5.32 and about 4.3 Ma.

The climatic variations along this sequence are slight. Annual temperatures were 1 to 6°C higher than today and precipitation 350 to 800 mm higher. So, during that period, there is a good correspondence between the climate of this region and of the Var region. Here the ratio E/PE is also high, coherent with the presence of a Taxodiaceae forest (mainly *Sequoia*-type; Suc et al., 1995b).

4.1.4. Roussillon (southern France)

For this region, just south of Languedoc, five relatively short records were available. The boreholes in Perpignan, Mutualité Agricole F1 (Cravatte et al., 1984) covering the period from about 4.8 to 4.5 Ma, and Canet 1 (Cravatte et al., 1984; Suc et al., 1995a)

covering the period from about 5.32 to 4.5 Ma. The sites Vivès and Le Boulou (Suc, 1989; Suc et al., 1995a) together with Nidolères (Suc, 1976) cover the period from about 5.1 to 4.9 Ma.

All these sequences are dominated by arboreal taxa at the beginning of the Pliocene, particularly Pinaceae and Taxodiaceae. Taxodiaceae and other subtropical taxa such as *Engelhardia* and *Symplocos* are then progressively replaced in the pollen spectra by Mediterranean xerophilous taxa (*Olea*, *Phillyrea*, *Pistacia*, *Quercus ilex*-type), situated at a drier substratum, e.g. limestone.

Climatic variations are recorded along these sequences but generally, temperatures were equivalent to 6°C higher than today and precipitation was 350 to 600 mm higher. The values of E/PE, between 70 and 100%, are coherent with the presence of a forest in the region.

4.1.5. Catalonia (northern Spain)

This region is split into the Northwest and the Southwest Mediterranean (Suc, 1989), each represented by one site: Garraf (Suc and Cravatte, 1982) in the Northwest Mediterranean zone and Tarragona in the Southwest Mediterranean (Suc et al., 1995b). At Garraf subtropical trees were dominant, among them *Taxodium distichum*-type indicating swamp conditions, *Engelhardia*, and *Symplocos*. The end of the pollen sequence is marked by the decrease of arboreal taxa to the advantage of herbaceous taxa (notably *Artemisia*, Asteraceae), indicating the beginning of the first glacial–interglacial cycles (Suc and Cravatte, 1982). Conversely, Tarragona is characterised by a predominance of herbs (mainly Asteraceae and Poaceae). Some herbaceous taxa such as *Lygeum*, *Nitraria* and *Calligonum* have been found, indicating very dry and hot conditions. Today these taxa are found in North Africa under subdesertic conditions (Fauquette et al., 1998a). There are decreased values of arboreal pollen grains compared to the Northwest Mediterranean zone, predominantly Taxodiaceae, *Engelhardia* and deciduous *Quercus*, as before. The Mediterranean xerophytes are regularly represented in this pollen diagram. In fact, the pollen assemblages resemble the modern thermo-Mediterranean formation (Bessais and Cravatte, 1988).

The climatic reconstruction made from the sequence of Tarragona, covering the period from 5.32

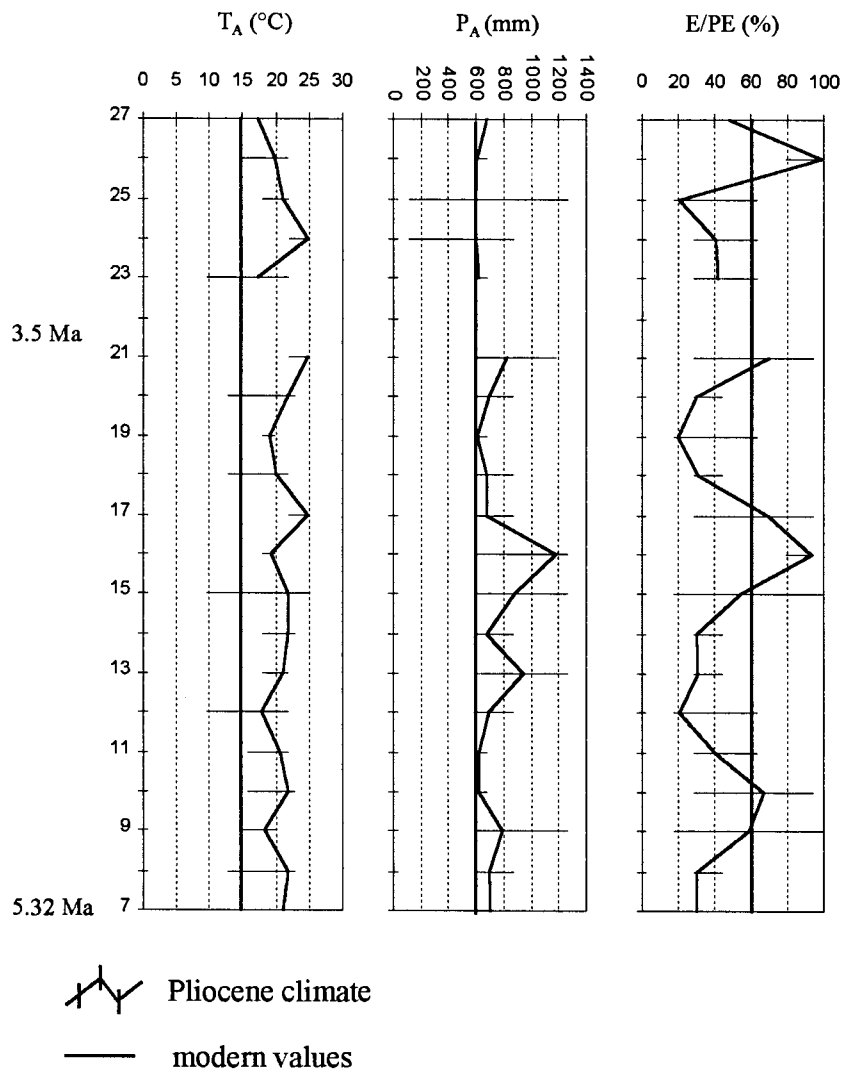


Fig. 4. Climatic evolution in Catalonia, at Tarragona during the Pliocene (between 5.32 and ~2.4 Ma).

to 3 Ma, shows temperatures between 1 and 10°C higher than today and precipitation equal to or higher than today (as much as 600 mm more) (Fig. 4). At Tarragona, the mixture of taxa of different vegetation types, subtropical trees and subdesertic herbs gives important variations in the climatic estimations from one spectrum to the next, particularly for annual precipitation and E/PE . Even with these variations, the amount of precipitation and the ratio E/PE are lower than at sites in the northwestern domain (in particular Garraf 1; Fauquette et al., 1998b), indicating the transition to a different climate regime. The climatic

estimations show an increasing latitudinal gradient both in temperature and dryness from north to south.

4.1.6. Andalucía G1 (southern Spain)

Situated further south, the composition of the pollen spectra at Andalucía is more or less similar to that of Tarragona, i.e. large quantities of herbs, including subdesertic herbs. Trees are well represented due to the presence of nearby relief.

Climatic fluctuations are recorded along the sequence of Andalucía (Fig. 5). The cooling event which occurred at around 4.5 Ma (Suc and Zagwijn,

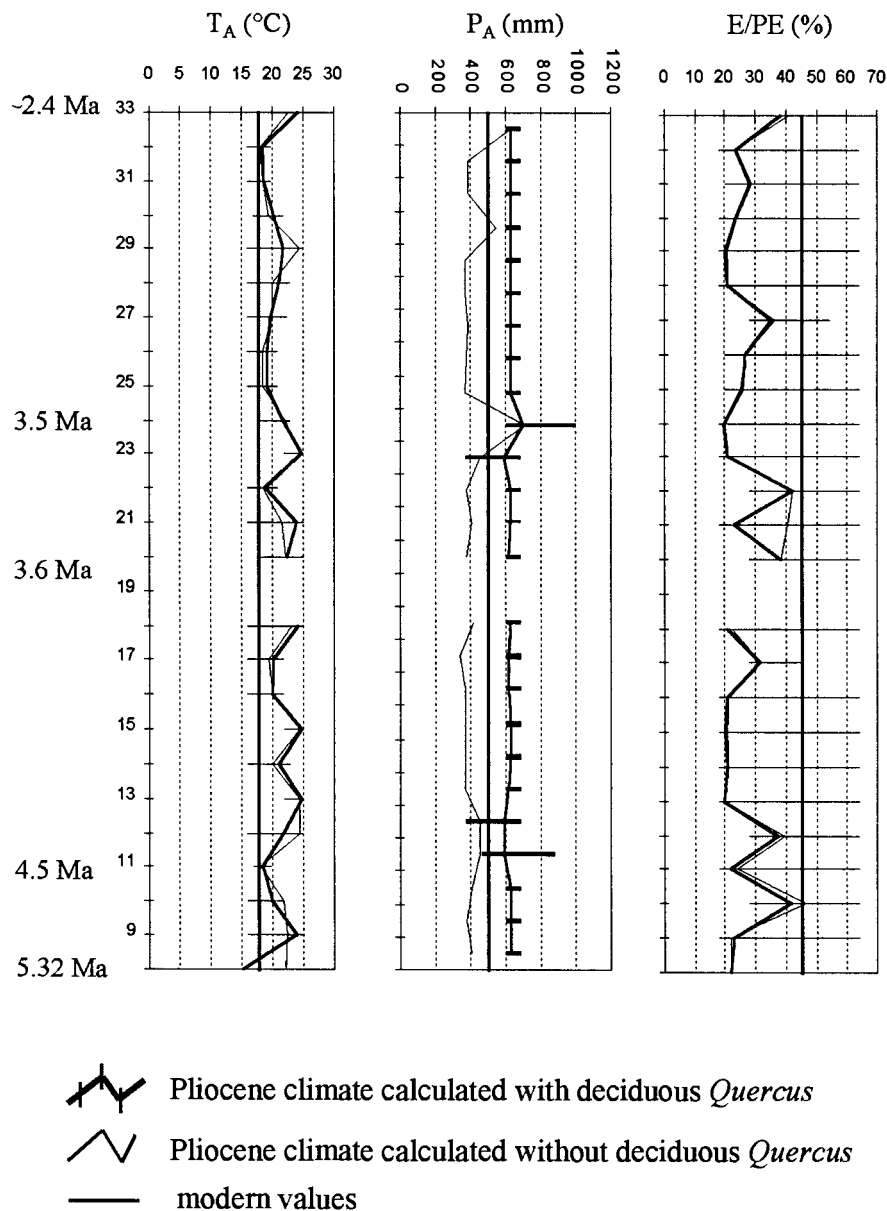


Fig. 5. Climatic evolution in Andalusia during the Pliocene (between 5.32 and ~2.4 Ma).

1983), and is recorded in the pollen data (Suc et al., 1995b), is evident in the mean annual temperature reconstruction (sample No. 11, where T_A is the same as today). Other less important oscillations follow this event and, finally, the decrease in temperature which occurs at samples Nos. 24 and 25 corresponds to the cooling that took place at 3.5 Ma (Zagwijn, 1960; Suc and Zagwijn, 1983; Suc, 1984). At An-

dalucia, annual temperatures were equivalent to 6°C higher than today. Some oscillations are recorded for the mean value of E/PE , but in general the interval is relatively stable with low values. Few changes are recorded for P_A , which was around 100 to 300 mm higher. In fact, the precipitation should be lower and may have been as low as it is under modern conditions. The spectra contain pollen derived from higher

elevations, in particular large amounts of *Quercus* (deciduous) pollen grains that grew at middle elevations. If deciduous *Quercus* is classified, for this site, in the 'C' group of taxa (high latitude/altitude taxa), the precipitation curve is shifted towards lower values (Fig. 5), which is more probable than the first calculated values. With this reclassification, no modifications are recorded for T_A and E/PE.

During the Pliocene, this region was characterised by a more or less similar vegetation type as today, i.e. an open subdesertic landscape (Suc et al., 1995b) but with more thermophilous taxa, found today in North Africa.

4.1.7. Nador 1

This site is situated at the North African sea-coast, on the opposite coast of the Andalusian site. The sequence of Nador begins at 5.32 Ma and is correlated to the Andalusian sequence by the foraminiferal stratigraphy (J. Cravatte, pers. commun., 1998). The most important differences between these two diagrams are the higher frequencies of subdesertic elements, Cupressaceae and steppic elements at Nador than at Andalusia. Again, the pollen diagram indicates an open subdesertic landscape, with the presence of deciduous *Quercus* growing at higher altitudes. The climatic estimations have been calculated, as for Andalusia, with deciduous *Quercus* in the 'C' group of taxa (Fig. 6). Annual temperatures were equivalent to 6°C higher than today and the annual precipitation was between the same as and 350 mm higher than today. The low values of the ratio E/PE confirm the hypothesis that a forest could not grow along the seacoast. A few minor climatic oscillations are recorded along the sequence but the first important one occurs just before 3.58 Ma (dated by biostratigraphy, J. Cravatte, pers. commun., 1998) and may correspond to the cooling taking place at 3.5 Ma (Suc et al., 1995b). According to the biostratigraphy, the first glacial–interglacial cycles begin before levels 18 and 19, perhaps at level 17 (Fig. 6) when the percentages of *Artemisia* increase.

4.1.8. Habibas 1

This site is situated in Algeria. Here again, herbaceous pollen were largely dominant, as it is today, notably Asteraceae, Poaceae and Amaranthaceae–Chenopodiaceae.

Climatic estimations have been calculated, as for Andalusia and Nador 1, with deciduous *Quercus* in the 'C' group of taxa. In our reconstruction, oscillations of annual temperatures are regularly recorded along the sequence, the significance of which is difficult to assess. In the upper part of the sequence, temperatures decrease toward the modern value (18.8°C). This may be attributed to the cooling event taking place at 3.5 Ma, and this has been confirmed by the biostratigraphy (J. Cravatte, pers. commun., 1998). Elsewhere in the sequence, temperatures were 6°C higher than today. Annual precipitation was very low and relatively stable along the sequence, at levels a little higher than today. The value of E/PE lies between 20 and 60%, with a most likely value oscillating between 25 and 45%, indicating very dry environments, where forest cannot develop, similar to today.

4.1.9. Oued et Tellil

This site in Tunisia is represented by a sequence covering a short period, from about 5.32 to 5 Ma (Suc et al., 1995b). The pollen data have been interpreted as a subdesertic landscape dominated by herbs such as Poaceae (including *Lygeum* which is represented by large amounts of pollen grains along the sequence), Amaranthaceae–Chenopodiaceae, Asteraceae, Plumbaginaceae and Geraniaceae, a typical association of very dry environments (Le Houérou, 1995). The two last spectra are marked by occurrences of Mediterranean non-subdesertic taxa, such as *Rhus*, *Vitis*, and *Olea*.

The climate appears stable along this sequence, but temperatures decrease at the end of the sequence when Mediterranean xerophytes appear. Annual temperatures were equal to or higher than today, from 19° to 25°C (19°C today), whereas annual precipitation and E/PE were lower than today (or equivalent), respectively between 300 and 450 mm (600 mm today) and between 20 and 60%.

4.1.10. Capo Rossello (Sicily)

The sequence of Capo Rossello covers a short period from 5.32 to 4.5 Ma and is represented by few pollen spectra. During this period, annual temperatures were similar to modern ones. The pollen spectra contain the same subdesertic plants as today, i.e. *Lygeum* and *Calligonum*; the fossil assemblages

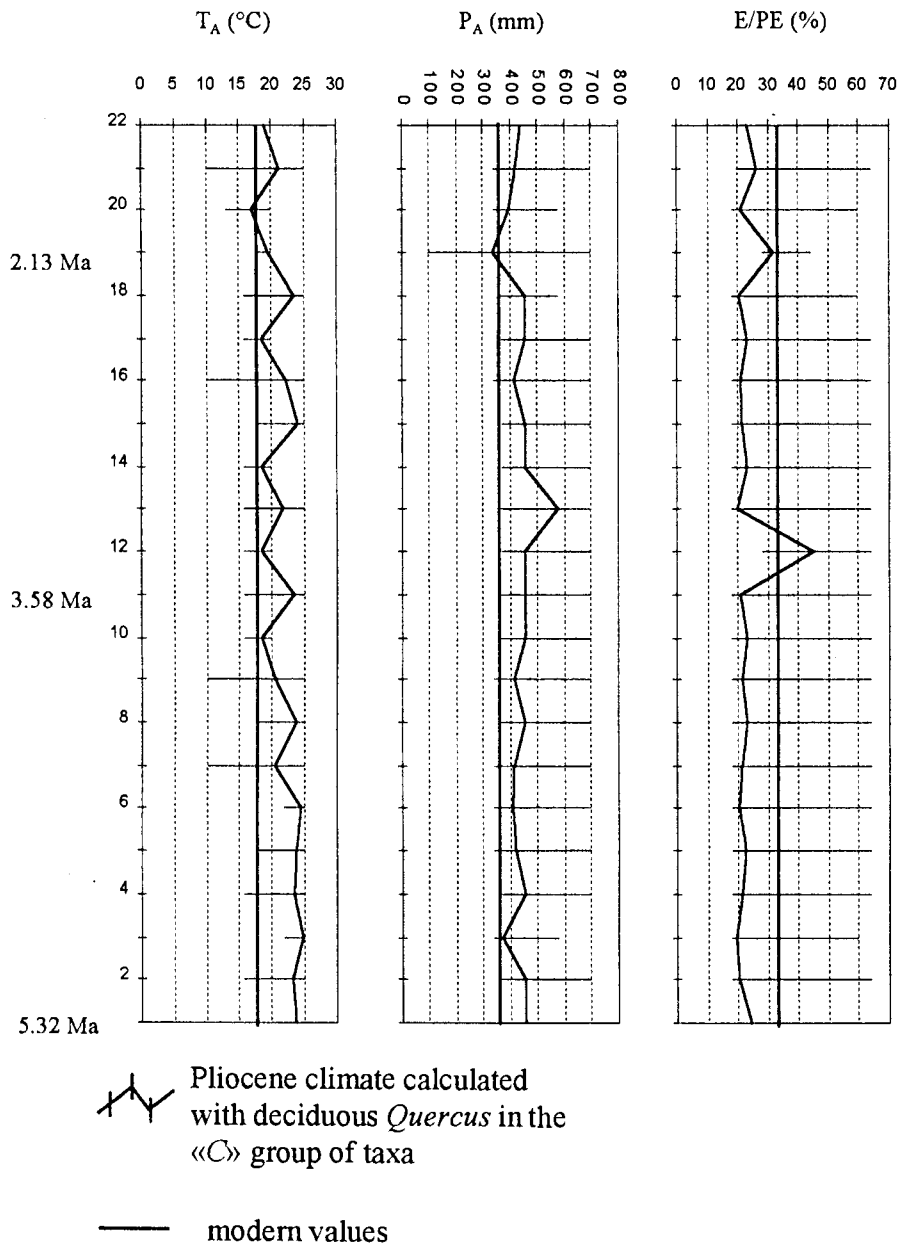


Fig. 6. Climatic evolution in North Africa, at Nador, between 5.32 and ~3.0 Ma, with deciduous *Quercus* in the 'C' group of taxa.

therefore appear to resemble the modern thermo-Mediterranean formation. Precipitation was slightly lower than today as was the E/PE ratio. One of the spectra contained occurrences of *Distylium*, *Engelhardia*, *Microtropis fallax*, *Parrotia persica* and *Ulmus*, indicating a less open environment at that time.

4.1.11. Rio Maior (Portugal)

This site is included in another, non-Mediterranean, vegetational domain: the West European zone. This zone differs from the other ones by the high representation of Ericaceae, which still characterises the Atlantic coast today (Oldfield, 1959). The

pollen diagram of Rio Maior (Diniz, 1984a,b) shows the dominance of subtropical trees (*Cathaya*, *Engelhardia*, *Sequoia*, *Myrica*, *Taxodium* ...). Mediterranean xerophytes such as *Olea*, *Phillyrea*, *Cistus*, Rhamnaceae and *Quercus ilex*-type were also well represented.

In this pollen diagram, montane elements such as *Abies*, *Tsuga*, *Sciadopitys* were weakly represented, thus indicating that relief was far away or else had no important influence.

The mixture of Mediterranean xerophytes and subtropical taxa shows a complex vegetation structure, which makes the reconstruction of climate difficult. Mediterranean xerophytes may have been either an integral part of the forest associations or already adapted to drier conditions, allowing colonisation of some areas, e.g. calcareous areas (Diniz, 1984a). This mixture of ecological types has resulted in the climatic variations seen in the reconstruction, particularly for annual precipitation and E/PE (Fig. 7). In

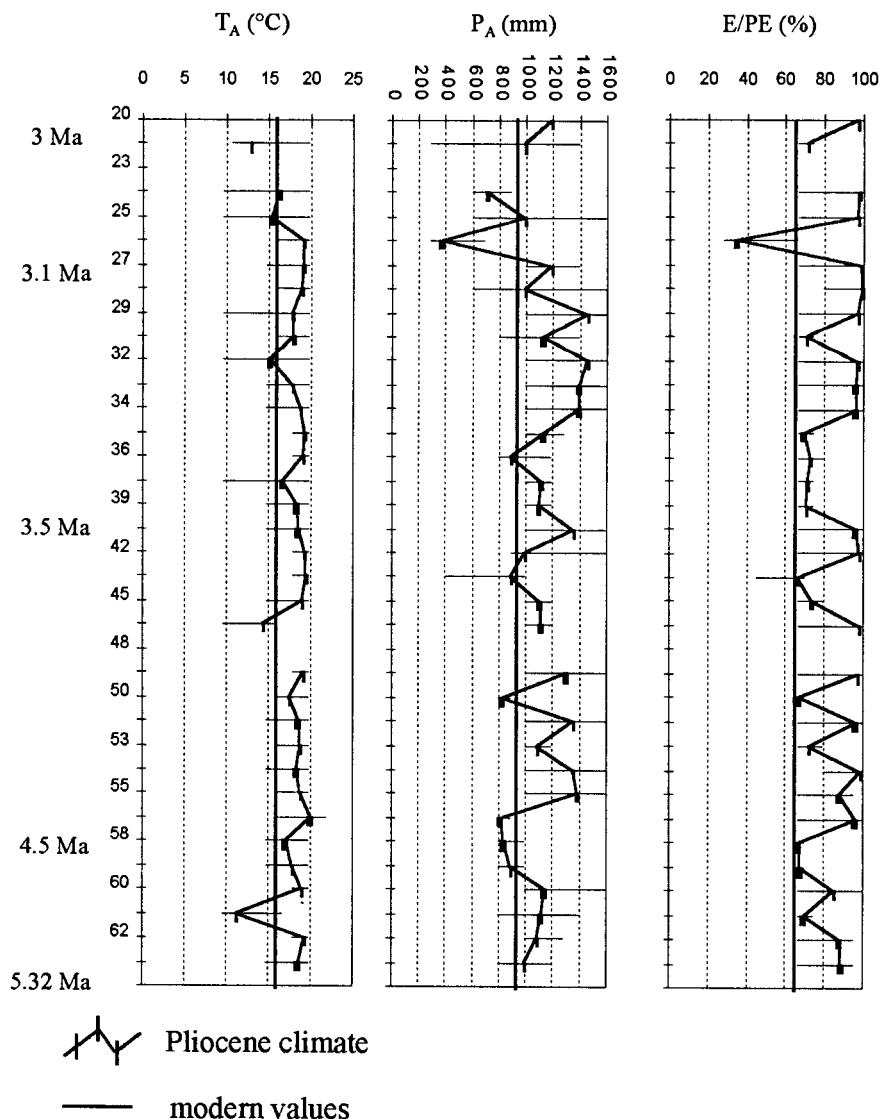


Fig. 7. Climatic evolution on the Atlantic coast, at Rio Maior, during the Pliocene.

general, annual temperatures and precipitation were equal or higher than today (respectively up to 4°C and 400 mm more than today). However, precipitation may have been lower than today, during phases characterised by high frequencies of Mediterranean taxa.

Neither our climatic reconstructions nor the pollen data (Suc et al., 1995a) show important changes at the period corresponding to the emergence of the Isthmus of Panama (4.6 Ma; Haug and Tiedemann, 1997). These authors have suggested that the closure of the seaway between the North and the South American continents modified the global thermohaline circulation, intensifying the Gulf Stream and introducing warm and saline water masses to high northern latitudes. They think that this phenomenon could favour, in particular, Early Pliocene warming of the high latitudes of the Northern Hemisphere and the increased availability of moisture. Although triggered by incremental changes in insolation, the closure of the Panamanian seaway was the ultimate cause of the progressive Pliocene intensification of the Northern Hemisphere glaciation (Hay, 1996). This finalised the Cenozoic cooling trend by the build up of the northern ice sheet.

At the same time, at 4.5 Ma, in the Mediterranean Sea, the presence of the foraminifer *Globorotalia puncticula* (Zachariasse and Spaak, 1983) marks the appearance of cooler conditions. However, this cooling is not recorded in every pollen sequence and thus in the climatic reconstructions.

The changes in Atlantic Ocean thermohaline circulation inferred from the formation of the Isthmus of Panama appear to be progressive. The resulting glacial phases appear to occur progressively, and do not always cause large changes in the vegetation.

From our reconstructions, the climate appears to be relatively stable during the period between 3.1 and 2.5 Ma, the period of intensification of Northern Hemisphere glaciation. This period seems to be characterised by a progressive cooling (Vergnaud-Grazzini et al., 1990; Tiedemann et al., 1994) which was not strong enough to rapidly or radically alter the vegetation. Therefore, as our reconstructions are based on variations of the vegetation composition, the slight climatic changes are not discerned.

4.2. The climate around the Mediterranean area at 5.32–5 Ma

For this period, the differences in vegetation due to latitude may be easily identified (Suc, 1989; Suc et al., 1995a). This is particularly notable between the Languedoc–Roussillon area and Catalonia, where the difference is marked by higher percentages of thermophilous plants to the south. The Mediterranean mixed forest of the northwestern domain gave way to Mediterranean open xeric assemblages in the lower latitudes. The latitudinal organisation of the vegetation appears, therefore, to be of ancient origin, although it becomes increasingly pronounced in recent periods. Since the Zanclean, a thermal threshold existed between Barcelona and Tarragona, as it does today, separating thermo-Mediterranean from meso-Mediterranean formations (Suc et al., 1995a).

In order to study this latitudinal gradient, climatic estimations have been calculated for all the sites covering the period 5.32–5 Ma (Fig. 8). At each site, the sum of three or four pollen spectra was used in the calculations, in order to have coherent values between all the sites.

The latitudinal climatic gradient seen in the pollen data is obvious in the reconstructions. Temperatures, precipitation and E/PE are similar at Saint-Martin du Var, Cap d'Agde 1 and Canet 1 (T_A from 15° to 17.7°C, P_A from 1180 to 1580 mm and E/PE from 79 to 100%). However, the site of Canet 1, characterised at that time by a higher level of Asteraceae and Amaranthaceae–Chenopodiaceae, appears a little drier than the other sites, with P_A around 1200 mm and E/PE between 66 and 100%. The climate at Garraf 1 was similar, i.e. warm and humid.

At Tarragona, a different type of climate was reconstructed, with higher temperatures and very low precipitation levels, between 575 and 880 mm (most likely value of 670 mm). These values are concordant with the change of vegetational zone: Tarragona is the northernmost site included in the Southwest Mediterranean zone. It is characterised by higher frequencies of herbaceous taxa and by the occurrence of some subdesertic taxa.

At Andalucia, south of Tarragona, precipitation is once again lower, between 300 and 700 mm (most likely value of 400 mm), but the temperatures are similar to those at Tarragona.

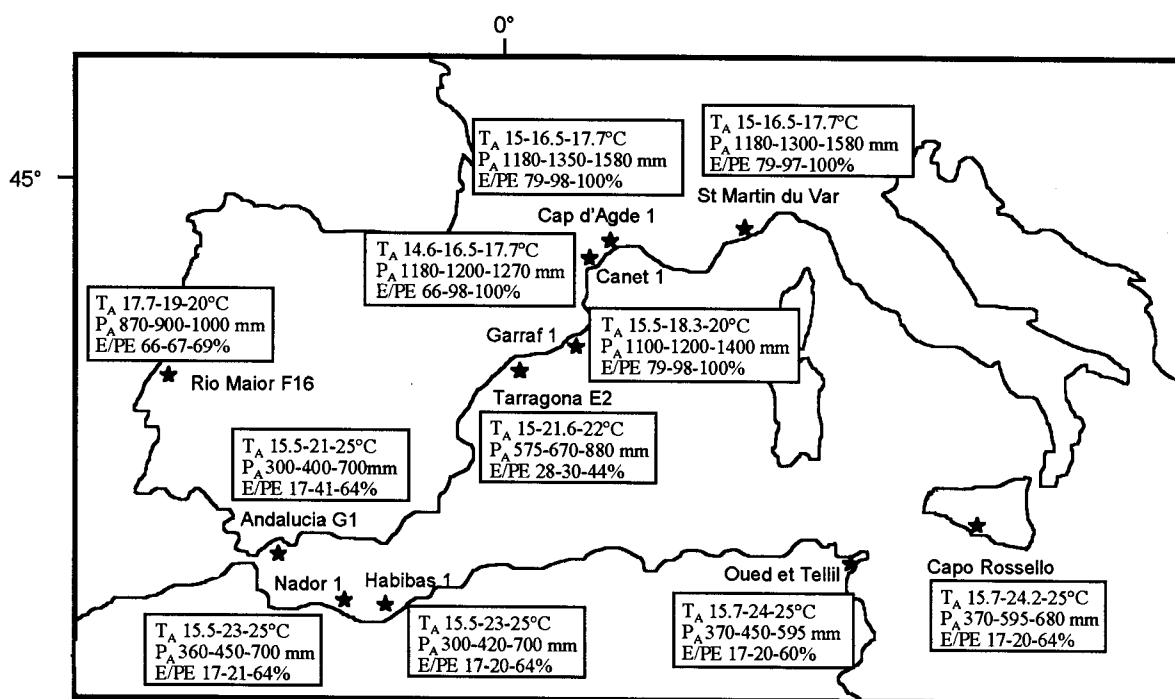


Fig. 8. Climatic variations around the West Mediterranean area at 5.32–5 Ma.

In North Africa (Nador, Habibas, Oued et Tellil) and in Sicily (Capo Rossello) temperatures are uniformly very high (T_A from 15.5° to 25°C with a most likely value of about 23°C). The very low values calculated for E/PE and annual rainfalls are consistent with the open vegetation type deduced from pollen data.

At Rio Maior, included in the West European vegetational domain, annual temperatures were between 17.7° and 20°C (most likely value of 19°C) and precipitation between 870 and 1000 mm (most likely value of 900 mm). These values are in agreement with the presence of both Mediterranean xerophytes and subtropical taxa, such as *Engelhardia*, *Nyssa*, *Symplocos*. The value of E/PE (between 66 and 69%) is also consistent with the presence of a mixed forest.

These results confirm that: (1) at 5.32–5 Ma, temperatures were higher than today (1° to 5°C on average), more notably in the Northwest Mediterranean area, precipitation was higher in the Northwest Mediterranean area and more or less similar to the modern one in the Southwest Mediterranean

area; (2) a climatic gradient from north to south existed at the beginning of the Pliocene, increasing for temperature and decreasing for precipitation; (3) the limit between the northwestern and the southwestern regions occurred between Garraf and Tarragona; the site of Rio Maior is distinct, coming under the Atlantic influence with a higher precipitation than at Tarragona or Andalucia.

The estimates are consistent with the climatic hypothesis of van der Hammen et al. (1971) that proposed a mean annual temperature ranging from around 11° to 16–17°C for the Netherlands during the Brunssumian (lower Pliocene) with high humidity.

Various mechanisms may be proposed to explain the differences between the Pliocene and the modern climatic situation in the West Mediterranean area.

(1) The existence of climatic forcing at a global scale; e.g. increase in solar radiation, increase of atmospheric CO_2 concentration, increase in ocean heat transport (Rind and Chandler, 1991) due to changes in the ocean's thermohaline circulation).

(2) An atmospheric circulation identical to today (i.e. zonal circulation), but shifted a few degrees in

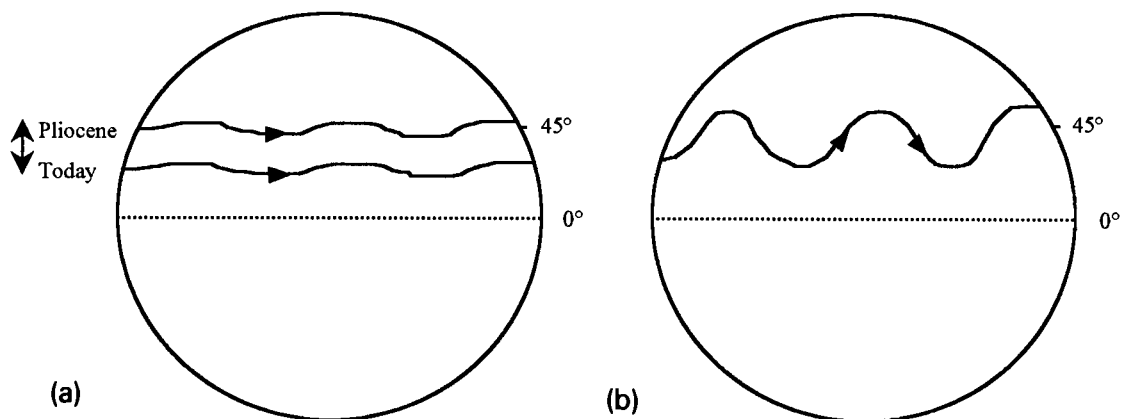


Fig. 9. Climatological hypothesis to explain the climate of the Pliocene: (a) same atmospheric circulation as today shifted to the north; (b) different atmospheric circulation with more accentuated waves.

latitude to the north (Fig. 9a). This would result in a northward displacement of the anticyclones situated today above the Saharan region at the beginning of the Pliocene. This would explain the higher temperatures but not the higher precipitation in southern France. On the contrary, the summer drought should have been more pronounced than today; this is not the case, however, as shown by the presence of the Taxodiaceae and other subtropical plants, despite a progressive increase in the summer drought (Suc, 1984).

(3) The atmospheric circulation may have been different, for example, with more accentuated waves of the jet stream (Fig. 9b). In such a case, the Mediterranean area would have been in a southwestern air flux which would have increased temperatures. Precipitations would also have been higher, particularly at the foot of mountains (e.g. in southern France). However, in this situation, some regions around the world, under the influence of northwestern air fluxes, would have lower temperatures than at present. Currently, all paleoclimatological studies for this period show temperatures more or less higher than at present (Edwards et al., 1991; Thompson, 1991; Dowsett et al., 1992; Willard, 1994). Not all areas of the earth have been explored and it may be that, currently, no paleoclimatological data exist for regions under the northwestern air fluxes.

Several other scenarios could be suggested but it is impossible to know at present the real cause of these climates. However, one of the most probable hypotheses is a combination of a global process

with the superimposition of another phenomenon (for example, a different atmospheric circulation).

Although no analogues of the Pliocene vegetation can be found today (in terms of pollen spectra), it is possible to find modern analogues of the Pliocene climate. Comparison of our climatic estimates with modern values gathered by Leemans and Cramer (1991) indicates where such climate types exist today. Based on the annual values of the different parameters, the climate existing in southern France at the beginning of the Pliocene may be found today in southern China (although the different precipitation regime must be taken into account), northern India, North America (in California or the southeastern states), South America (around Buenos Aires in Argentina), and in eastern Australia (close to the Tropic of Capricorn in Queensland). If only the lower value of the climate range is considered, a similar climate can be found in France (around Bordeaux). The climate estimated for the regions of Tarragona and Andalucia is found today in southern Europe (southern Spain, Greece, Cyprus), Syria and Lebanon, North Africa (e.g. northern Tunisia), Central Africa (Botswana, Zambia, if only the higher limits of the climatic estimations are considered), and in northwestern Mexico and southern Australia. Finally, the climate existing in North Africa during the Pliocene may be found today in northern Egypt and Libya, Namibia, the Sonora region in northern Mexico, central Australia, and also along the southwestern coast of Australia.

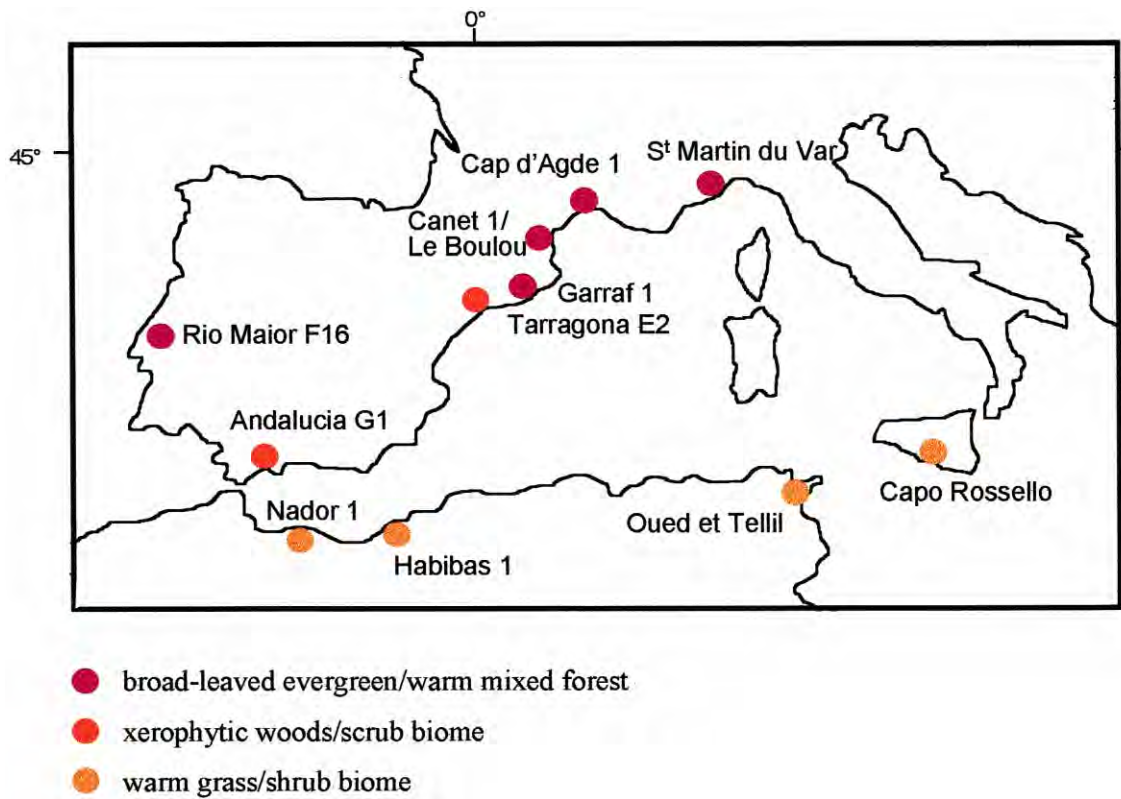


Fig. 10. Biome reconstruction at 5.32–5 Ma using the typology established by Prentice et al. (1992), our climatic estimations, and the vegetation description based on pollen data.

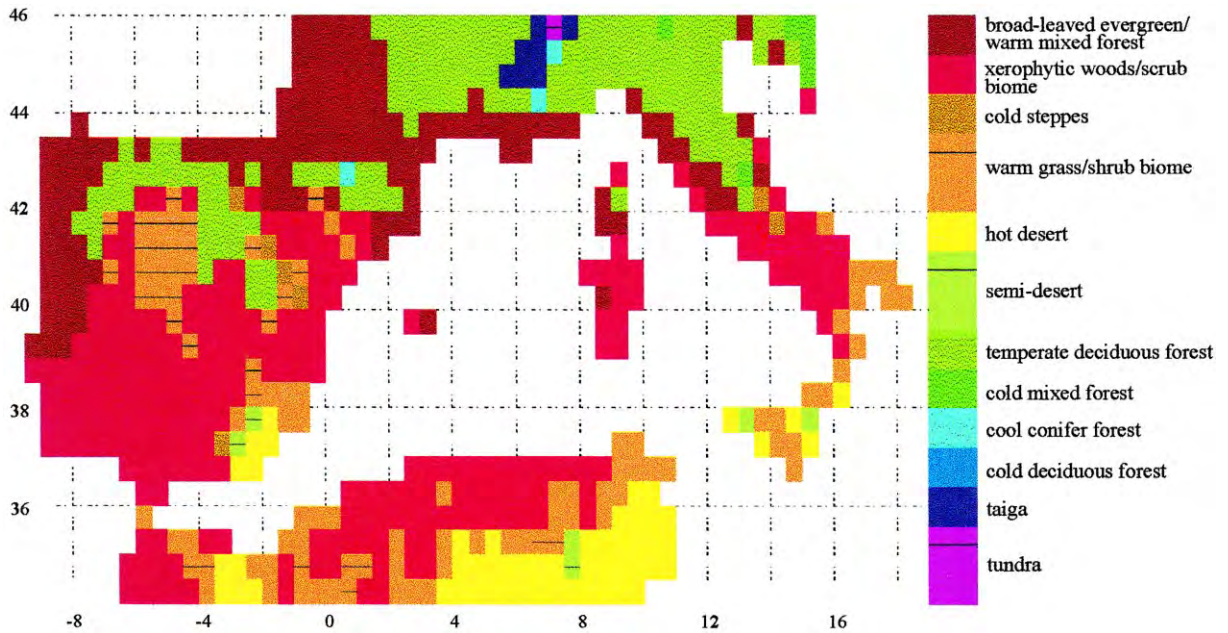


Table 1

Reconstruction of the E/PE ratio, of the mean temperature of the coldest month (T_C) and of the warmest month (T_W) for the West Mediterranean area at 5.32–5 Ma

Sites	E/PE (%)			T_C (°C)			T_W (°C)		
Saint-Martin du Var	79	97	100	5	6.6	9.8	20	22.6	24.6
Cap d'Agde 1	79	98	100	5	8	9.8	15	20	24.6
Canet 1	66	98	100	4.5	9.4	14	19.8	25	26.8
Garraf 1	79	98	100	5	9.8	14.6	24.6	25.8	26.6
Tarragone E2	28	30	44	5	14.5	16	24.6	25.5	26
Andalucia G1	17	41	64	7.3	10.5	14.6	22	25	28
Nador 1	17	21	64	7.3	12	14.6	22	25.5	28
Habibas 1	17	20	64	7.3	12	14.6	22	25.2	28
Oued et Tellil	17	20	60	7.3	9.4	14.4	22.8	25.9	27.7
Capo Rossello	17	20	64	7	12	14.4	22	26	28
Rio Maior F16	66	67	69	9.8	11.5	14.6	24.6	25.2	26.6

For each parameter, the first and the third values correspond, respectively, to the lower and the upper limits of the estimated climatic interval. The second value corresponds to the weighted mean of the interval.

5. Biomes around the Mediterranean area at 5.32–5 Ma

The estimation of biomes for a given region enables climate modellers to improve their models by establishing more precise boundary conditions for that region. A biome reconstruction for the period 5.32–5 Ma around the Mediterranean area has been attempted, using the typology established by Prentice et al. (1992). These reconstructions are based on the climatic estimates of the temperature of the coldest month, of the warmest month and the E/PE ratio (Table 1). A biome has been assigned to each site according to the climatic parameter limits established by Prentice et al. (1992). This assignation was further determined by using the vegetation description based on the pollen data. The environmental constraint values of Prentice et al. (1992) were used to determine biomes corresponding to the pollen spectra, compatible with both our climatic estimations and the vegetation composition.

Three biomes have been found at 5.32–5 Ma at the different sites studied: the broad-leaved evergreen/warm mixed forest, the xerophytic woods/scrub

biome and the warm grass/shrub biome (Fig. 10). The climatic and vegetational criteria that define these biomes are the following.

(1) The broad-leaved evergreen/warm mixed forest is indicated when the temperature of the coldest month ranges from 5° to 15.5°C and E/PE is above 65%. This biome includes all vegetation types where warm-temperate evergreen trees, whether broad- or needle-leaved, are dominant (Prentice et al., 1992). At the beginning of the Pliocene, this biome is represented in the south of France where *Taxodiaceae* forests are dominant and it resembles the broad-leaved evergreen/warm mixed forest found today in eastern China or in California. It can be also attributed to Rio Maior where subtropical taxa are largely dominant, although the Mediterranean assemblages were more important. This biome was also found at Garraf. The *Taxodium* swamps, which characterised this site, were due to particular local edaphic conditions (Suc and Cravatte, 1982). Today, this biome is found in the south of France, but with lower temperatures and precipitation.

(2) The xerophytic woods/scrub biome is defined by the dominance of tall xerophytic plants (i.e.

Fig. 11. Map of the interpolated biomes at 5.32–5 Ma. First, anomalies between Pliocene and modern climate have been calculated and then interpolated on the Leemans and Cramer (1991) grid to obtain the Pliocene climate for the whole grid. According to these results, using the scheme of the Biome 1 model (Prentice et al., 1992), biomes are reconstructed around the Mediterranean Sea.

Mediterranean sclerophyllous shrubs, succulents and tropical thorns), temperature of the coldest month above 5°C and E/PE between 28 and 65%. This biome occurs where the climate is too dry for warm-temperate evergreen trees. Xerophytic woods/scrub biome can be attributed to the sites of Tarragona and Andalucia where Mediterranean taxa are well represented and where the climatic values established by Prentice et al. (1992) are respected. Once again the limit between the northern and the southern parts of the West Mediterranean region is well-defined. This biome is still represented in these regions with more or less similar annual rainfall but lower temperatures.

(3) The warm grass/shrub biome occurs under climates with a temperature of the warmest month higher than 22°C and a very low value of E/PE (between 18 and 28%). This biome is attributed to sites where vegetation corresponds to an open xeric environment. All these characteristics are found at Capo Rossello and in the sites in North Africa (Nador, Habibas and Oued et Tellil). This biome occurs today to the south of these sites or in subdesertic regions in central Spain.

The boundary conditions necessary for climate models can be interpolated from these data on a regular grid around the Mediterranean area, using the climatic data gathered by Leemans and Cramer (1991). Anomalies between Pliocene and modern climate are calculated (for T_C , T_W and E/PE) and then interpolated on Leemans and Cramer's grid. By adding these anomalies to the modern climatic values of Leemans and Cramer (1991), we obtain the Pliocene climate for the whole grid. Then, using the scheme of the Biome 1 model (Prentice et al., 1992), biomes have been reconstructed around the Mediterranean Sea (Fig. 11).

At the beginning of the Pliocene, the North African coast appeared to be covered by two biomes, the warm grass/shrub biome and the xerophytic woods/scrub biome. However, there are not enough sites along the coast to confirm the occurrence of this last biome. In Sicily, two biomes were represented: the warm grass/shrub biome, and the hot desert biome which occurs when the temperature of the warmest month is higher than 22°C and E/PE is comprised between 0 and 18% (Prentice et al., 1992). Sicily was thus very close to North Africa, from a climatic and vegetational point of

view. In Spain, between Tarragona and Andalucia, the biome was principally the same as today, i.e. a xerophytic woods/scrub biome, despite higher temperatures. Some other biomes occurred locally (the warm grass/shrub biome and the hot desert), but the paucity of data prevents any confirmation of this.

North of Tarragona the biome changed at the same limit as today, as the broad-leaved evergreen/warm mixed forest succeeded the xerophytic woods/scrub biome. It covered the whole southern France and probably extended northward into Europe; again, the lack of data prevents any confirmation. In northern Italy, Bertini (1994) indicated that the vegetation was a mixed mesophytic forest, with the presence of subtropical and warm-temperate elements. The author mentions that the Italian Zanclean sections are characterised by the abundance of Taxodiaceae, and by the scarcity of herbaceous plants, similar to that seen in the Ligurian (Zheng, 1990) and French sections (Suc, 1976, 1981; Cravatte et al., 1984; Zheng, 1990). The author mentions also that the sections are strikingly different from those found at Capo Rossello (Suc and Bessais, 1990). Thus, the biome attributed to the northern Italian coast (the broad-leaved evergreen/warm mixed forest) using the interpolation technique is consistent with the qualitative interpretation of the Pliocene data. It is hazardous to attribute a biome to central and southern Italy, as no data are available for these regions. Moreover, geomorphologic studies suggest that only a part of central Italy had emerged (Boccaletti et al., 1990). Lastly, the Atlantic coast of the Iberian Peninsula is covered by two biomes: the broad-leaved evergreen/warm mixed forest to the north and the xerophytic woods/scrub biome to the south. Rio Maior is placed at the limit between these two biomes, which is consistent with the oscillations between the Mediterranean xerophytes and the subtropical plants seen in the pollen diagram (Diniz, 1984a).

Using this technique, a biome has been attributed to each grid cell. It must be stressed that the interpolation is based on only ten Pliocene sites for the whole West Mediterranean area and the results are perhaps wrong for regions where no corroborative data exist. Further, precise limits between the biomes cannot be established (except between the North and the South Mediterranean regions, i.e. between Tar-

ragona and Barcelona, because of the proximity of these two sites). If, however, we assume that climatic changes are homogeneous within a large region and that lapse rates have not changed we can be reasonably confident in this distribution of the biomes.

Attempts have been made to relate the Mediterranean Pliocene with modern vegetation. For example, the Pliocene vegetation described for southern France has been compared to Chinese and to Californian modern vegetation (Zheng, 1990). The biome reconstruction realised in this study confirms this previous work, as the broad-leaved evergreen/warm mixed forest is present today in California and China (southern and eastern China). Initially, the comparison with the Chinese vegetation appeared to be the most accurate as there is a large number of Pliocene taxa in China. However, in terms of climatic conditions and geographic location (i.e. the west side of a continent), the Californian model seems better related. The eastern Chinese coast is under monsoon influence with a maximum rainfall during the summer, the contrary of California. During the Pliocene in Europe and in the Mediterranean region, the presence of Mediterranean taxa indicates that there was no monsoon regime. The Californian model, therefore, may be closer to the Pliocene vegetation type.

6. Comparison with simulations of the Pliocene climate

A great number of models have been used by the members of the PMIP (Paleoclimate Modeling Intercomparison Project) to simulate the climate for some phases of the Quaternary period. For the Pliocene, a model has been established by the Goddard Institute for Space Studies (GISS). The aim of the GISS is to develop tools for simulating future climate change. Predictions of future changes gain credibility when models can accurately simulate changes that have occurred in the past. Whilst the climate of many past time periods has been simulated, the most interesting periods to simulate are those during which the average global temperature was more than 1°C higher than today. These periods may resemble the future climate on Earth, if the increased greenhouse effect is taken into account. The Early Pliocene appears to be the more appropriate period, as we have calcu-

lated temperatures of 1° to 6°C higher than today in the Mediterranean region.

Chandler et al. (1994) have used the GISS General Circulation Model and data generated or compiled by the PRISM (Pliocene Research, Interpretation and Synoptic Mapping) project (pollen data, dinocysts, foraminifers, ostracodes and diatoms). The boundary conditions of one of their simulations are deduced from reconstruction of Pliocene SST, terrestrial vegetation and modern geographic conditions (topography, land ice, Southern Hemisphere SSTs, atmospheric conditions . . . , M. Chandler, pers. commun., 1998). Although these simulations do not constitute a full Pliocene reconstruction, it is interesting to compare them to our results. A difficulty in comparing the sets of results is the grid cell size of the model simulation ($7.83^\circ \times 10^\circ$) which encompasses vast areas: the area studied in this paper is divided into just six grid cells in this model (Fig. 12).

For the Northern Mediterranean sites, the simulated annual temperatures are close to the values reconstructed from pollen data, even for the southwestern European region (cf. Rio Maior). For the annual precipitation, the comparison is more complicated. The model results are good for the grid cell corresponding to the site Saint-Martin du Var and also for the Atlantic coast of the Iberian Peninsula. The results are less good for the central grid cell where the simulation gives an annual precipitation value that is too low at Cap d'Agde, and a value too high for the region of Tarragona. This grid cell covers two different vegetational and climatic domains, which are merged in the climatic simulation.

For the Southern Mediterranean sites, the annual temperature simulation fits well with the values obtained from pollen data for the three grid cells. However, the GISS model gives values of annual precipitation which are too high and not compatible with the vegetation type deduced from pollen data (subdesertic vegetation). Here again, the cause of these discrepancies is probably the size of the grid cells, which encompasses more humid mountainous regions.

The values of T_C and T_W have been also compared to our estimations but the results of the simulations are not good for these parameters. Their T_C estimates are too high and the T_W estimates, whilst better, are often too low, which implies an over-reduced thermic seasonality.

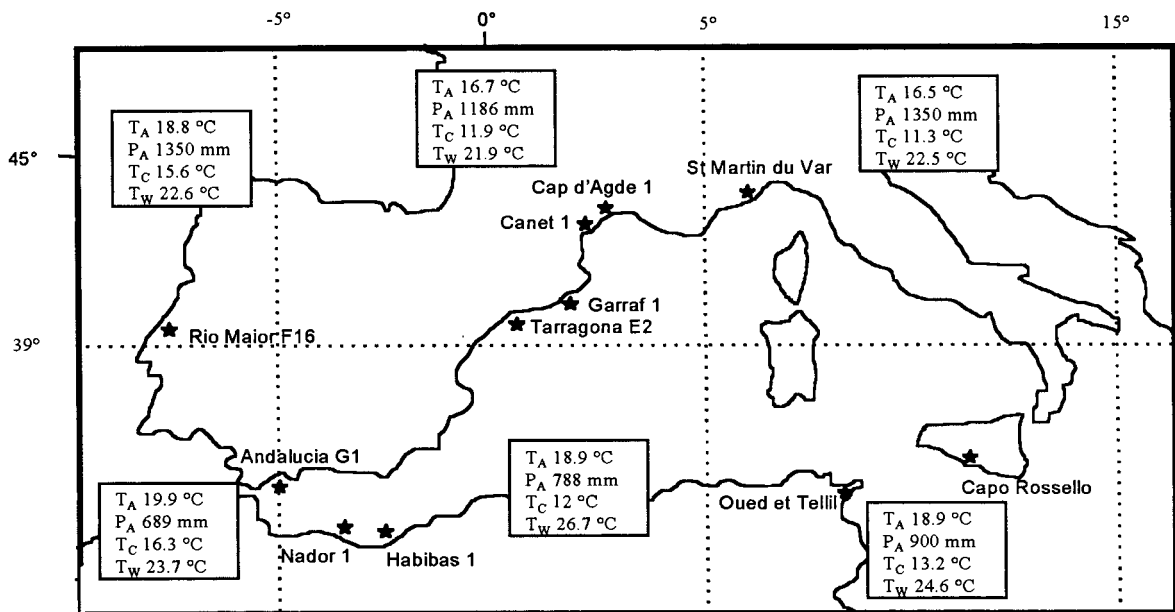


Fig. 12. Climatic estimations obtained with the GISS model (M. Chandler, pers. commun., 1998). The resolution of the grid cell is $7.83^\circ \times 10^\circ$.

Although the results of this model represent a first and non-complete approach to the simulation of the climate of the Pliocene, the comparison with our results shows some agreement for T_A and P_A for almost all the Mediterranean region. A higher-resolution grid would allow better simulations and perhaps a closer fit to the data-based estimates.

A new model experiment is currently being carried out with full Pliocene paleogeographic reconstructions and a variety of experiments testing the model's sensitivity to various climate-forcing mechanisms, e.g. atmospheric CO_2 and ocean heat transport (M. Chandler, pers. commun., 1998). This may yield results better correlated with the estimations obtained from the pollen data.

7. Conclusion

The climatic estimations calculated for the West Mediterranean Pliocene show that temperatures and precipitation were higher than today, especially in the North Mediterranean domain. The climate was, on average, warm and humid in the North Mediterranean domain (respectively 1° to $4^\circ C$ and 400 to 700 mm higher than today), and warm and dry in

the South Mediterranean domain (respectively equal to or $5^\circ C$ higher and drier than or equal to today). At Rio Maior, situated in the Atlantic domain, the climate was warmer and drier than in the North Mediterranean area but colder and more humid than in the South Mediterranean domain.

The latitudinal gradient of climate that is revealed by the pollen data (one of the starting points of this climatic quantification) is clearly visible in our reconstructions. The direction of this gradient appears to be similar to today, i.e. the climate was warmer and drier in the South than in the North Mediterranean domain.

Following the environmental constraints of Prentice et al. (1992), biomes were defined for each site for the period 5.32–5 Ma. The biomes were reconstructed using the climate estimate obtained earlier in the study, together with a description of the vegetation, based on the pollen flora. For this period in the Mediterranean region, three biomes have been identified: (1) the broad-leaved evergreen/warm mixed forest which was dominated by Taxodiaceae, resembling the broad-leaved evergreen/warm mixed forest found today in eastern China or in California; (2) the xerophytic woods/scrub (dominance of tall xerophytic plants) which occurred where the climate

was too dry for warm-temperate evergreen trees; and (3) the warm grass/shrub biome corresponding to an open xeric environment.

These biomes have been interpolated along the West Mediterranean littoral, on a regular grid, using T_C , T_W and E/PE estimates. Anomalies between Pliocene and present-day climate have been calculated and then interpolated for the Mediterranean region. It is obvious that precise limits between the biomes cannot be determined, unless two biomes are represented by sites in close proximity, e.g. the limit between the North Mediterranean (Tarragona) and the South Mediterranean (Barcelona).

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A new approach for palaeoaltitude estimates based on pollen records: example of the Mercantour Massif (southeastern France) at the earliest Pliocene

Séverine Fauquette^{a,*}, Georges Clauzon^b, Jean-Pierre Suc^c, Zhuo Zheng^d

^a Institut Méditerranéen d'Ecologie et de Paléoécologie, UPRES-A CNRS 6116, Case 451, Faculté des Sciences de Saint-Jérôme,
13397 Marseille cedex 20, France

^b CEREGE, UMR CNRS 6635, Europôle de l'Arbois, BP 80, 13545 Aix-en-Provence cedex 04, France

^c Centre de Paléontologie Stratigraphique et Paléoécologie, ERS CNRS 2042, Université Claude Bernard-Lyon I,
69622 Villeurbanne cedex, France

^d Faculty of Geology, Zhongshan University, 510275 Guangzhou, China

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Abstract

The altitude of the Mercantour Massif (Southern Alps, France) during the earliest Pliocene has been estimated using a new quantification method. Instead of classical methods using geomorphologic criteria, our method uses biogeographic and climatologic criteria: composition of the modern vegetation belts in the European and peri-Mediterranean mountains, and Pliocene annual temperature estimates obtained from fossil pollen data. The climatic transfer function indicates for the coastal earliest Pliocene of the studied area a mean annual temperature of 16.5°C. Such a temperature today occurs at 38.5°N latitude in the Mediterranean region. The relation established by Ozenda between the present-day vertical and latitudinal vegetation assemblages evidences a shift of, on average in Western Europe, 110 m in altitude per degree in latitude. As a consequence, it is possible, taking into account that the Pliocene lapse rate was almost similar to the modern one, to estimate the minimum altitude of the massif at the earliest Pliocene. The so-obtained palaeoaltitude estimate is close to that obtained with the geomorphological method: the Mercantour Massif was almost 2000 meters high at the earliest Pliocene. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: altitude; Southern Alps; lower Pliocene; pollen; climate; geomorphology

1. Introduction

Quantification of palaeoaltitudes is of first importance: (1) in the estimation of the rate of orogenesis, (2) in the evaluation of erosional input into the flux of terrigenous sediments accumulated in the sedi-

mentary basins [1], and (3) in the elaboration of palaeoclimatic models [2].

Several geological approaches to this problem can be used, such as geomorphology or the analysis of erasure kinetics of fission tracks in apatites [3]. Fission tracks form spontaneously in apatites by fission of ²³⁸U. They may be erased completely or partly according to rock temperature: erasure is complete when the temperature is above 120°C but non-exis-

* Corresponding author. Tel.: +33 491 2885 27; Fax: +33 491 2886 68; E-mail: severine.fauquette@lbhp.u-3mrs.fr

tent when the temperature is under 60°C. Between 60 and 120°C, the higher the temperature the shorter the length of fission tracks formed. The knowledge of the laws of the erasure kinetics of tracks experimentally determined, allows the reconstruction of the thermal history of a massif from the distribution of the track length. This results in indices of the importance of denudation as a consequence of erosion, and thus provides inferences about the previous altitudes of mountains.

We have developed a new method, based on pollen records and climatic reconstructions. Some attempts have already been carried out using palaeofloras, especially macroremains, to estimate past altitudes [4–7]. The above-mentioned palaeoaltitude estimates have appeared complicated to calculate, more especially as these authors apply it to periods far from the Present, which implies important palaeogeographic differences. Moreover, their methods concern vegetal macroremains that provide a fragmentary and very circumscribed idea of the vegetation. In addition, these macrofloras are located at mid to high altitude in the western United States and have no direct link to the altitudinal climatic gradient of the seashore. This imposes the need to have two coeval floras (one at the seashore and the other one at a higher altitude) that is very rare [4–7].

Our new method takes into account pollen floras accumulated near the coastline which provide a regional view of the vegetation from the littoral up to the uppermost altitudinal belts. The first example concerns the Southern Alps, northward of Nice (Fig. 1) at the earliest Pliocene (5.32–5.1 Ma), where validation can be carried out by geomorphology.

In order to improve our knowledge of the Mediterranean palaeogeography during the Miocene–Pliocene we need reliable estimates of relief elevation. The Alpine major tectonic phases are chronologically relatively well constrained. The best data come from the West and Central Alps [8,9] where the latest tectonic phase belongs to the Lower Miocene. On the other hand, the recent evolution of the chain, which is characterised by vertical movements [8] is very poorly known. So, it is very important for the understanding of the Southern Europe geodynamics to propose reliable palaeoaltitudes that can be compared to the GPS and fission track measurements in process.

2. Palaeogeographical context

Today the Mercantour Massif in southeastern France reaches its highest point at 3143 m, less than 50 km from the Mediterranean Sea coast (Fig. 1). This steep slope extends offshore: abyssal plains of 2000 m depth occur less than 80 km from the Alpine crest line. With a drop of 5000 m, it represents the most important altitudinal contrast in the Western Mediterranean.

Different means of reconstruction [10,11] indicate that the bathymetry of the basin resembled the modern one at the beginning of the Messinian salinity crisis (at about 5.8 Ma). During this important event, the desiccation of the Mediterranean Sea margins was due to a glacio–eustatic sea-level fall that was followed by the tectonic closure of the straits connecting the Mediterranean Sea to the Atlantic Ocean [12]. This has led to strong regressive erosion [13–15] with the cutting of deep canyons by rivers, as the Var River has into the Southern French Alps [12,16,17].

The abrupt earliest Pliocene flooding of the Mediterranean Basin at 5.32 Ma (to about 70–80 m above the present-day sea-level [18]) generated deep sedimentary basins (Zanclean rias). The filling of the rias formed Gilbert deltas [19] that are characterised by the superposition of two stratigraphic units which are back to back: the basal unit, deposited in a sub-aquatic environment, is open toward downstream (bottom-set and fore-set beds), whereas the overlying unit, deposited in a sub-aerial environment, is open toward up-stream (top-set beds) [20]. The underlying unit includes detritic (sands and/or gravels) fore-set beds with an important sedimentary dip (20 to 30°); downwards, bottom-set beds (hemipelagic clayey facies, rich in fossils) succeed these fore-set beds. The overlying unit corresponds to an alluvial fan cone with a weak sedimentary dip (i.e. top-set beds).

Such a structure is interesting for two reasons:

(1) From a palaeogeographic point of view: it gives a good record of the contemporaneous eustatic level. The marine/continental transition takes place at the interface of the sub-aquatic and sub-aerial units. It is characterised by a dip rupture between the fore-set beds and the top-set beds.

(2) From a chronostratigraphic point of view: the Var/Tinée Gilbert delta construction lasted the whole

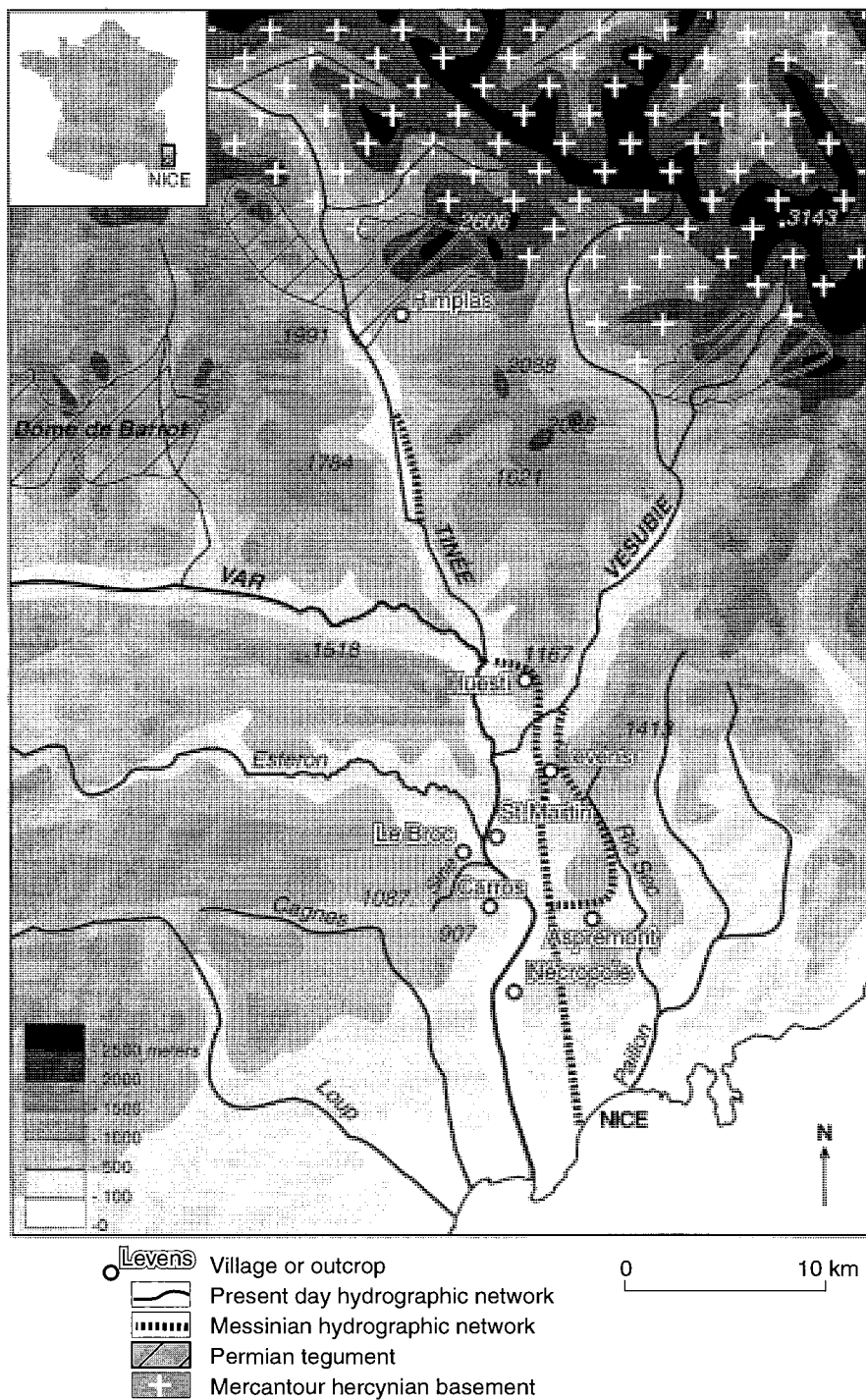


Fig. 1. Location map of the studied area showing the important slope from the sea to the summits of the mountains (Mercantour Massif, southeastern France), which are less than 50 km from the sea.

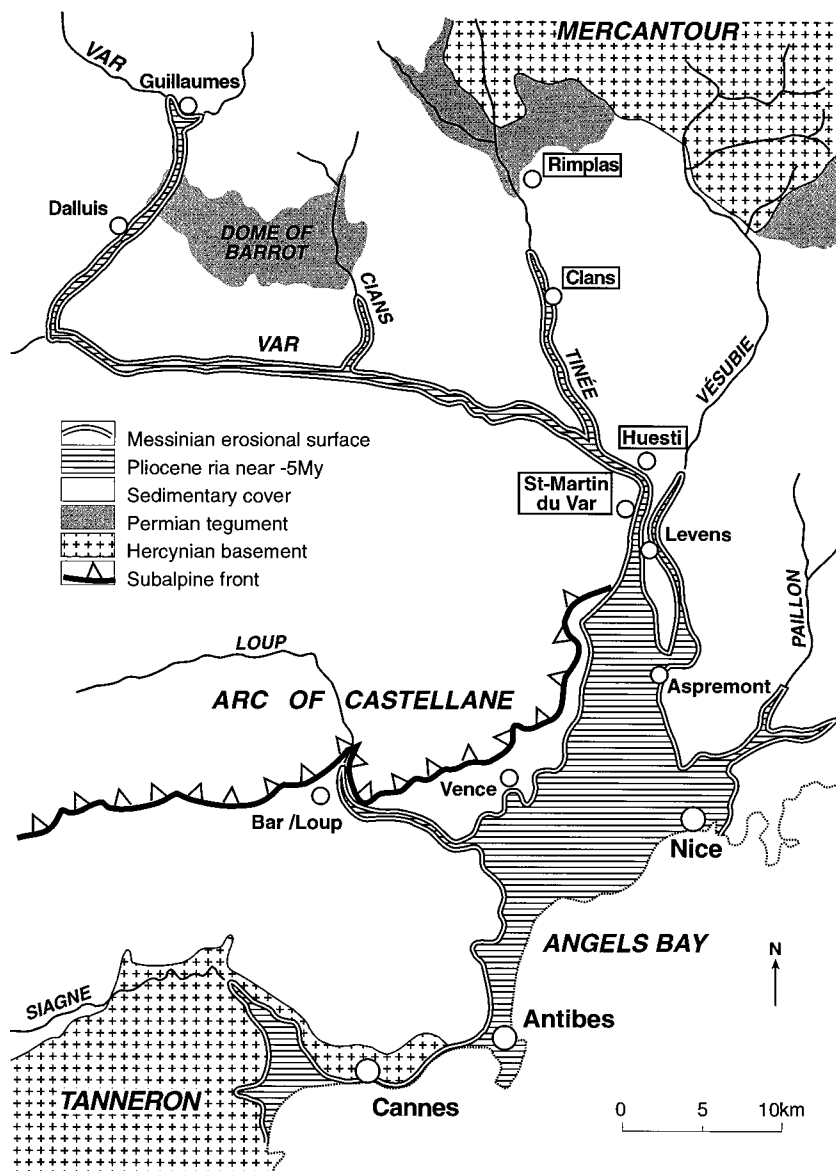


Fig. 2. Map of the Var ria at the beginning of the Pliocene (at around 5.32–5 Ma) and location of Saint-Martin du Var.

Pliocene. It started during the maximum flooding of the earliest Pliocene (5.32 Ma), as shown by the microfauna of Saint-Martin du Var (*Sphaeroidinellopsis* acme-zone [21,22]), and it ended, according to the presence of *Globorotalia inflata* at the distal part of the Gilbert delta [22], during the late Pliocene, i.e. at ca. 2.0 Ma. The earliest Pliocene flooding created a new palaeogeography since the coastline in the ria heads was located very close to the Alpine mountain front.

The Var and the Tinée rias penetrated the Alpine mountains (Fig. 2), respectively 20 km northward of Nice and 42 km northward of the Modern sea coast, between Clans and Rimplas [12,17]. The transition marine/continental has been preserved upstream, at the head of the Tinée ria. This transition has not been preserved downstream but the Pliocene eustatic level can be defined on rocky coast by saxicavous molluscs. As a consequence, a reconstitution of the

Pliocene marine/continental transition is possible for the whole length of the ria. This reference plane permits us to estimate the subsequent deformation and also to determine, by a retrospective investigation, the morphology and structures sealed in the Pliocene Gilbert delta (Fig. 3).

From a eustatic point of view, the Lower Pliocene is marked by a high marine level (cycles of third order: TB 3.4/3.5 of the Vail Charter) [18]. At the end of this cycle, the Gilbert delta occupied 3/5 of the ria, the head of the ria being at Aspremont, less than 15 km from the Modern coast line.

3. Biogeographical and climatic context

With the aim of describing the Pliocene vegetation of Southern France, fossil pollen was analysed from clays sampled at Saint-Martin du Var (Fig. 1), north of Nice [22,23]. These sediments (about 60 m thick) were deposited during the maximum flooding of the earliest Pliocene, in a littoral zone bordered with mountains. They correspond to deltaic sediments, the pollen flora of which provides an overview of vegetation from coastline to altitudinal belts because of the prevailing pollen transport by rivers [24,25].

The pollen diagram (Fig. 4) which covers the earliest Pliocene, between 5.32 and ~5.1 Ma, according to biostratigraphy and geology [22,23], points to a forest environment. From low to mid altitude, the forest was mainly composed of Taxodiaceae (*Sequoia*-type pollen grain), *Pinus p.p.*, which is always over-represented in marine coastal sediments due to its prolific pollen production, its good preservation and over-abundance in air and water transport [24–26], *Cathaya*, *Engelhardia*, deciduous *Quercus*, *Ulmus*, etc. The abundance of *Sequoia*-type pollen grains reflects the presence of homogeneous forests on the slopes immediately from the coast [23], based on the Modern Californian model [27]. At higher altitude, the forest was richer in altitude elements like *Pinus p.p.*, *Abies* and *Picea*. Mediterranean xerophytes were little represented and certainly located near the seashore. The very low representation of herbaceous taxa in pollen spectra argues for a very narrow coastal plain. The mountain front was thus certainly very close to the littoral zone. *Abies* and *Picea* were probably well represented at

a relatively short distance from Saint-Martin du Var. Their percentages respectively range between 1 and 5% (*Abies*) and 1 and 2% (*Picea*). *Abies* has been recorded (0.33%) in a Modern marine surface sample near the mouth of the Var (core KNI31, IFREMER Nicasar cruise; Suc, unpublished), which means a slight representation at only 60 km from its nearest biotope (Fig. 5). For comparison, Modern pollen records in the Rhône delta (pollen rain traps at La Tour du Valat and La Palissade, Modern sediments from core KTR05 [25]) show low percentages of *Abies* (less than 2%) and *Picea* (between 3 and 4%) relatively far from the source localities (Fig. 5).

Climatic reconstructions have been made on the basis of the pollen spectra, using a new method of climate quantification (a ‘mutual climatic range method’), especially carried out to reconstruct the Pliocene climate [28,29]. In contrast to the ‘best analogues method’ [30], this technique allows us to reconstruct the climate of periods without Modern vegetation analogues; it is based on the transposition of climatic requirements of a maximum of Modern plants to fossil data. Indeed, ecological homologies between Pliocene and Modern taxa are usually accepted [31,32], more especially as palynologists work more often at the genus level of identification. The earliest Pliocene climate has been estimated on the sum of the whole pollen sequence of Saint-Martin du Var, which represents about 200,000 years according to biostratigraphy [22].

At the beginning of the Pliocene, the climate at Saint-Martin du Var was warmer and more humid than today. At sea level, mean annual temperatures were about 16.5°C (between 15 and 17.7°C, i.e. 1–4°C higher than today); rainfall was about 1300 mm (between 1200 and 1500 mm, i.e. 500–800 mm higher than today); the available moisture was also higher than today, falling between 79 and 100% [33]. These climatic conditions promoted the development of subtropical plants in this region.

4. Palaeoaltitude estimate of the Mercantour Massif during earliest Pliocene time: palynological evidence

Altitudinal zonation of plants reflects to their latitudinal distribution. For example, the *Abies*–*Picea*

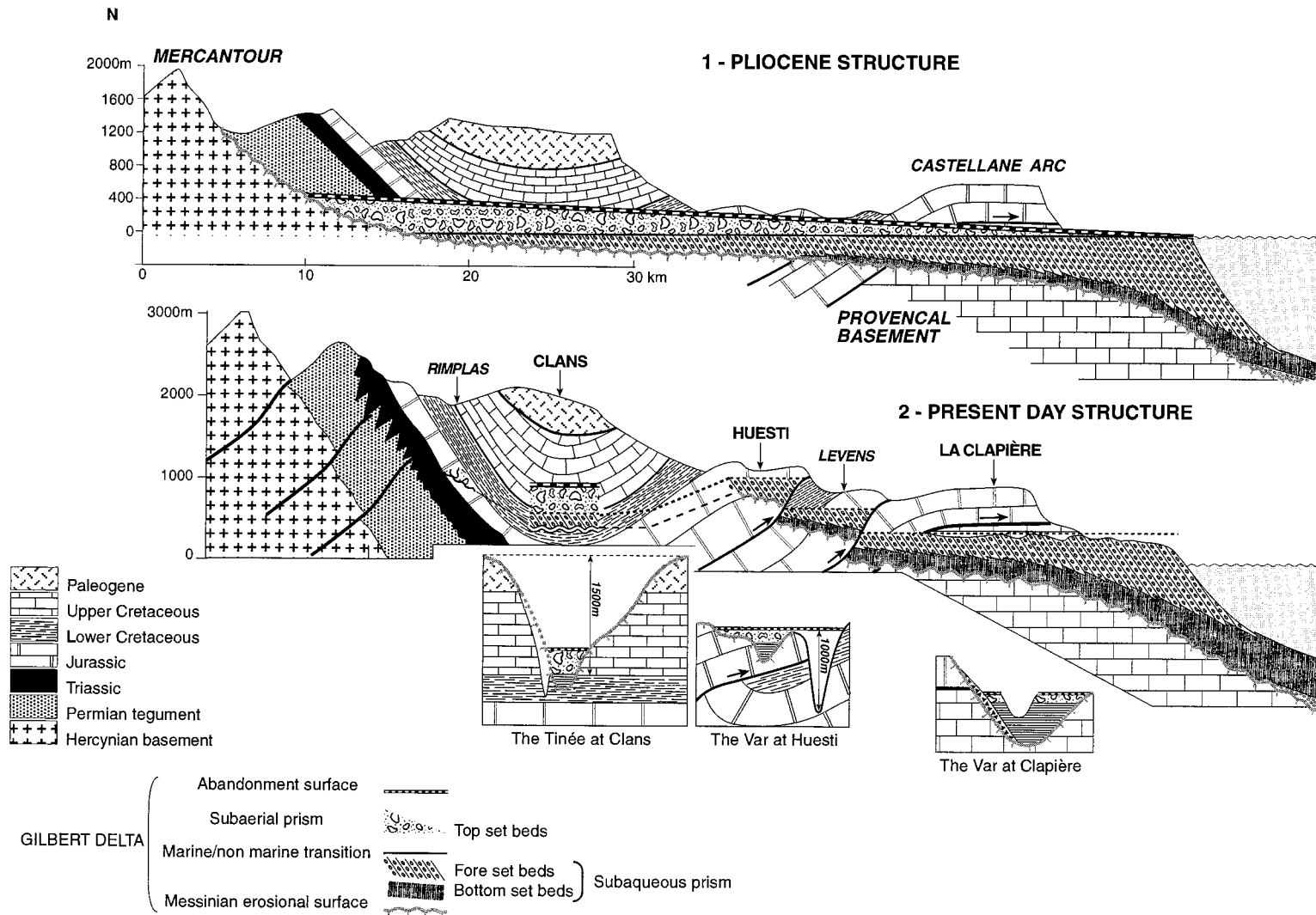


Fig. 3. The Pliocene Gilbert delta of the Var river: (1) at the end of its construction (at around 2.0 Ma) and (2) today.

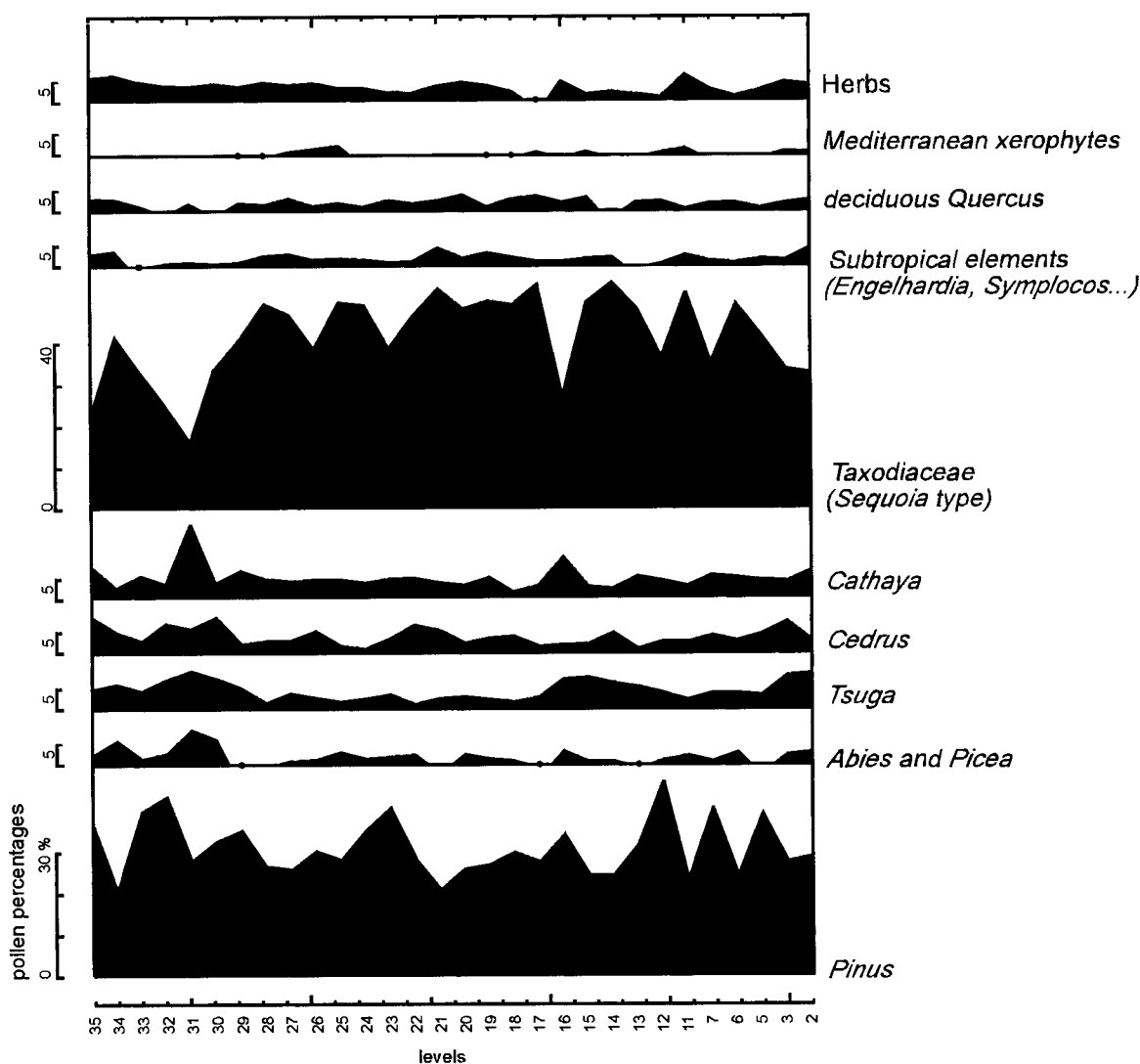


Fig. 4. Pollen diagram of Saint-Martin du Var (only curves of the main taxa or groups of taxa are represented). This pollen sequence does not cover more than 200,000 yr: the bottom of the sequence corresponds to the beginning of the Pliocene (~ 5.32 Ma) and the top of the sequence does not reach 5.1 Ma according to biostratigraphy (the foraminifer *Globorotalia margaritae* is not present in the top samples [22]).

belt occurs between 0 and 500 m altitude in southern Sweden and southern Norway [34], but is situated between 1400 and 2000 m in the southern French Alps [35] (Fig. 6). The vertical shift of the vegetation belts in relation to latitude is obvious but difficult to quantify, as the altitudinal range of plant species is controlled not only by climatic parameters (decreasing temperature and increasing precipitation

with altitude), but also by local conditions (nature of soils, slope orientation). Ozenda [36] attempted to quantify this vertical shift in Europe according to three observations: (1) vegetation belts occur at different altitudes at different latitudes; (2) in temperate regions, mean annual temperatures vary about 0.6°C per degree in latitude (1° in latitude = ca. 110 km); (3) temperature decreases in relation to the altitude

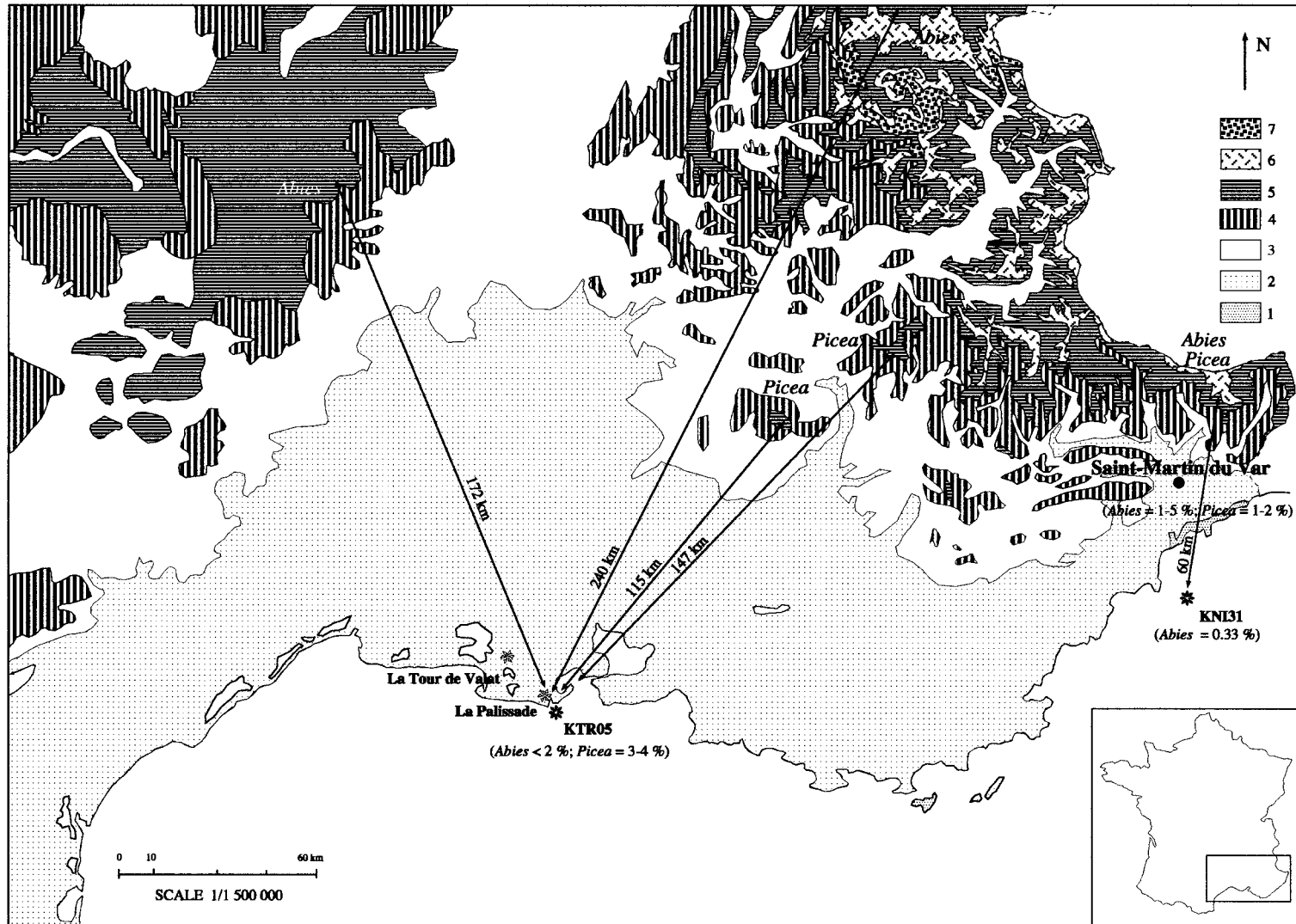


Fig. 5. Vegetation map of southern France [34] and representation of *Abies* in Modern pollen spectra (cores KTR05 and KN131, pollen rain traps of La Tour du Valat and La Palissade) and in fossils pollen spectra (Saint-Martin du Var) to show the distance between the sources of altitude taxa pollen grains and the sedimentation site. Modern vegetation belts: 1 = Thermomediterranean; 2 = Mesomediterranean; 3 = Supra-Mediterranean; 4 = Mountainous (*Fagus*); 5 = Subalpine (*Abies*, *Picea*, *Larix*); 6 = Alpine (herbs); 7 = continuously snow-covered.

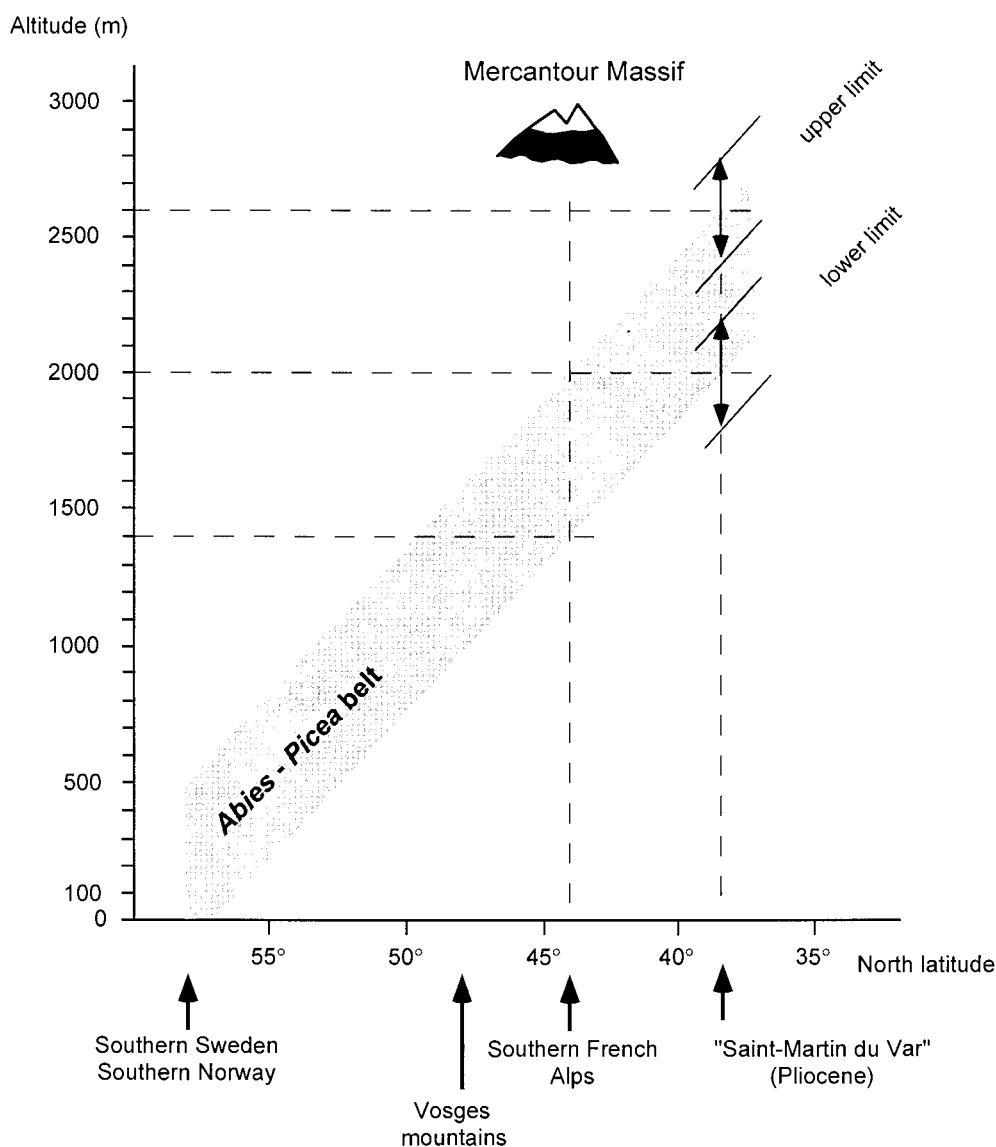


Fig. 6. Altitudinal variation of the *Abies*–*Picea* belt in relation to latitude, from North to South, and estimation of the palaeoaltitude of the Mercantour Massif, taking into account the Modern altitude of the *Abies*–*Picea* belt in the South French Alps and the higher temperature during the Pliocene.

at about 0.55°C per 100 m of elevation. Ozenda [37] established the following relation: a shift of 1 km to the North is equivalent, from a bioclimatic point of view, to a shift of 1 m in altitude. So today, in general, vegetation belts shift 110 m in altitude per degree in latitude.

Using this relation, the vegetation distribution and the climatic estimations, it is possible to estimate

the altitude of the Mercantour Massif at the earliest Pliocene:

- at that time, the mean annual temperature at Saint-Martin du Var, situated at 44°N latitude, was about 16.5°C on the coastline (range comprised between 15 and 17.7°C), according to estimates from pollen data. Today, such a temperature occurs southward of Valencia in Spain, at about

38.5°N latitude at sea level, about 5.5° lower in latitude from Saint-Martin du Var (or else between 3.5 and 8° lower in latitude if we consider the range of estimated temperatures);

- using the relation established by Ozenda, a shift of 5.5° in latitude corresponds to a shift of about 605 m in altitude. Thus, at the earliest Pliocene, vegetation belts should have shifted about 600 m (or 400–800 m according to the above-mentioned confidence interval) higher;
- today, the lower altitudinal limit of fir (*Abies*) in the Mercantour Massif is situated at about 1400 m [35]. Taking into account the shift of 600 m in vegetation belts between today and the earliest Pliocene, fir has occurred from about 2000 m (or 1800 to 2200 m). This means that, at the beginning of Pliocene, the Mercantour Massif was almost 2000 m high above sea-level.

5. Palaeoaltitude estimate of the Mercantour Massif: geomorphological evidence

In the case of the Mercantour Massif, this minimum estimated altitude can be validated. On the basis of geomorphological data, it is possible to estimate the palaeoaltitude of the Mercantour Massif at the earliest Pliocene, using the restitution of the marine/continental transition made for the Pliocene sedimentary filling of the Var and the Tinée rias (Fig. 3). Southward of Clans [12], this transition is observed at 580 m elevation. The Tinée ria, with a North/South orientation in this area, orthogonally intersects a large syncline which comprises sediments from Triassic to Oligocene age. The Annot sandstone ledge overhangs this thick sedimentary series, reaching 2085 m at Mont Tournairét. Assuming that the syncline crest had not been eroded since its Messinian shaping, then, at around 5 Ma, it was already overhanging the sea-level of the ria by almost 1500 m (2085 m minus 580 m). Expressed by reference to the modern sea-level, the difference in altitude is 1570 m (the high sea-level of the 3.4 cycle being situated at +70 m) [18].

The syncline crest of the Tournairét was situated, by definition, downward of the intumescence of the Hercynian basement, which has led to its formation by inducing the slip-off and flexure of the sediment

cover. In its modern disposition, the Mercantour Hercynian basement constitutes a sliced deep fold, rejuvenated during the Quaternary [38–41]. The basement is closed in its northwestern part by a pericline ending of the Meso–Cenozoic sedimentary cover. In this area, at Saint-Etienne de Tinée, the radius of the basement anticline is about 1000 m. Southward at Saint-Sauveur de Tinée (exactly in the studied area), it reaches 1600 m.

At around 5 Ma, the major part of the geological structure was already acquired, as shown by the incision of the Messinian canyon of the Tinée river which cuts the pre-Pliocene deposits at 1500 m depth (see detail on Fig. 3: ‘the Tinée at Clans’). Nevertheless, it appears that a tilting of 3–4° marks the Mercantour structural block. This is particularly obvious at the Pliocene marine/continental transition, which originally was horizontal. This disposition reveals a recent uplift, the value of which is calculated at 500 m when projecting the angle of 3–4° on the Mercantour Massif (10 km northward). Thus, the vertical distance between the tops of the Mercantour Massif and the Clans anticline must be reduced by 500 m, which represents half of its present-day value.

This estimated minimal value allows us to say that the Mercantour Massif was, at the earliest Pliocene, almost 2100 m high. Moreover, this palaeogeographic restitution indicates also that the Plio–Pleistocene uplift of the Mercantour was about 1000 m.

6. Discussion and conclusion

Our method, developed to reconstruct palaeoaltitudes, does not consider a possible difference between today and Pliocene lapse rates. Past lapse rate is difficult to estimate because it depends on many factors (atmospheric conditions, in particular atmospheric CO₂ level, albedo of the ground surface, moisture). Pliocene lapse rate could be slightly different than today, particularly because CO₂ level was slightly different [42–44]. We have considered that the lapse rate is almost unchanged since the Pliocene. This assumption is supported by two arguments: (1) the Pliocene latitudinal vegetation succession through Europe [45] was almost similar to the

Modern one in northwest America; (2) the climatic transfer function evidences a Pliocene thermic latitudinal gradient through Europe parallel to the Modern one but at higher level of values.

The estimation of the altitude of the Mercantour Massif from pollen and climatic data is a minimum value. It is impossible to deduce the actual altitude of mountain through this method. Indeed, pollen data do not allow establishment of the altitudinal range of the *Abies* belt, nor whether the alpine herbaceous and perpetual-snow belts above it existed. Elements of the alpine belt cannot be distinguished on their pollen from herbaceous taxa growing within the other vegetation belts (including the coastal one). The only data available correspond to the minimum altitude of *Abies* in the Alpes-Maritimes (i.e. 1400 m). In fact, just north of Nice, *Abies* can now be present at low altitude (from 700 m) in certain situations, such as well-shaded north-facing slopes [46]. However, in the Mercantour Massif, the co-occurrence of *Abies* and *Picea* is only found above 1400 m (Fig. 5) [47]. We assume that Pliocene *Abies* pollen grains were provided by populations growing at high altitude for the following reasons: (1) in the pollen spectra, *Abies* is associated to *Picea* (high altitude and/or latitude taxa); (2) the sediments deposited at Saint-Martin du Var in the Pliocene rias were transported by three rivers, the Var, the Vesubie and the Tinée (Fig. 2); today, upstream, *Abies* is present up to 1400–1500 m but not at a lower altitude; (3) at the earliest Pliocene, the mountain front was near the site, with a restricted coastal plain. Numerous low altitude taxa are present in the pollen spectra (deciduous *Quercus*, *Engelhardia*, *Ulmus*, ...), indicating that these taxa grow on slopes up to the middle elevations, thus limiting *Abies* and *Picea* to higher altitudes.

If we suppose, a priori, based on the geomorphological evidence, that an alpine belt existed during this period [35], then the Mercantour should have been 2600 m high (or 2400 to 2800 m, taking into account the reconstructed climatic interval).

So, the palaeoaltitude of the Mercantour Massif can be estimated by comparison with the Modern altitudinal distribution of the *Abies*–*Picea* belt, taking into account that the climate during the Pliocene was warmer than today (Fig. 6).

The new method developed to obtain palaeoaltitude estimates, based on pollen data and climatic

reconstructions, is very simply to use, because it just needs values of temperature at sea-level for a given region at a given period. Then, owing to the relation established by Ozenda, one can obtain the palaeoaltitude of this region.

This first attempt of quantification of palaeoaltitude has been realised on the Southern Alps at the earliest Pliocene, because for this region and this period a control may be obtained using geomorphological reconstructions.

One may note that these two ways give similar results. In the two cases they correspond to minimum values, but they give a good idea of the importance of the high relief at that time. The Mercantour Massif was almost 2000 m high at the beginning of the Pliocene.

These estimates constitute a first attempt for a given region and a given period. Now this method has to be applied to other regions and/or other periods.

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Latitudinal climatic gradients in the Western European and Mediterranean regions from the Mid-Miocene (c. 15 Ma) to the Mid-Pliocene (c. 3.5 Ma) as quantified from pollen data

S. FAUQUETTE¹, J.-P. SUC², G. JIMÉNEZ-MORENO³, A. MICHEELS⁴, A. JOST⁵,
E. FAVRE², N. BACHIRI-TAOUFIQ⁶, A. BERTINI⁷, M. CLET-PELLERIN⁸, F. DINIZ⁹,
G. FARJANEL¹⁰, N. FEDDI¹¹ & Z. ZHENG¹²

¹*Institut des Sciences de l'Evolution de Montpellier, UMR CNRS 5554, case courrier 061, Université de Montpellier II, Place Eugène Bataillon, 34095 Montpellier cedex 5, France (e-mail: fauquet@isem.univ-montp2.fr)*

²*Laboratoire Paléoenvironnements et Paléobiosphère, UMR CNRS 5125, Université Claude Bernard - Lyon1, Boulevard du 11 Novembre, 69622 Villeurbanne cedex, France*

³*Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuente Nueva S/N, 18002 Granada, Spain; Department of Earth and Planetary Sciences, Northrop Hall, University of New Mexico, Albuquerque, New Mexico 87131 and Center for Environmental Sciences & Education, Box 5694, Northern Arizona University, Flagstaff, AZ 86011, USA*

⁴*Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany*

⁵*UMR CNRS 7619 Sisyphe, Université de Paris VI, Case 105, 4 Place Jussieu, 75252 Paris Cedex 05, France*

⁶*Département de Géologie, Faculté des Sciences de Ben M'Sik, Université Hassan II – Mohammedia, BP 7955 Sidi Othmane, Casablanca, Morocco*

⁷*Università degli Studi di Firenze, Dipartimento di Scienze della Terra, Via G. La Pira 4, 50121 Firenze, Italy*

⁸*Morphodynamique continentale et côtière, UMR CNRS 6143, Université de Caen, 24 rue des Tilleuls, 14000 Caen, France*

⁹*Departamento de Geologia, Universidade de Lisboa, 1294 Lisbon codex, Portugal*

¹⁰*Rue du Faubourg Bonnefoy, 31500 Toulouse, France*

¹¹*Département des Sciences de la Terre, Faculté des Sciences, Université Caddi Ayyad, Avenue Prince Moulay Abdellah, BP S15, Marrakech, Morocco*

¹²*Department of Earth Sciences, Zhongshan University, 510275 Guangzhou, China*

Abstract: In Europe and the Mediterranean region, the vegetation and climate of the Neogene is well understood, due to the abundance of pollen data, allowing the climate evolution at a time of global cooling to be described. This paper presents a climatic reconstruction of four key time-slices of the Neogene: the Mid-Miocene (c. 14 Ma), the Late Miocene (c. 10 Ma), the Early Pliocene (c. 5–5.3 Ma) and the Mid-Pliocene (c. 3.6 Ma). The results show that Neogene climate was warmer than today and that the transition from a weak latitudinal thermic gradient (around 0.48 °C/degree in latitude) to a gradient similar to that of today (0.6 °C/degree in latitude) took place at the end of the Miocene. The latitudinal precipitation gradient was more accentuated than today from the Mid-Miocene to the Mid-Pliocene, with higher precipitation than today in northwestern Europe and the northwestern Mediterranean but with conditions that were drier than or equivalent to today in the southwestern Mediterranean region.

The Neogene is a period of intense climatic changes, from the 'greenhouse' climate of the Early to Middle Cenozoic to the 'icehouse' climate of the Late Cenozoic (Zagwijn 1960; Shackleton *et al.* 1995; Suc *et al.* 1999), and many factors, such as atmospheric CO₂, orbital parameters, ocean heat transport and palaeogeographical modifications, may have played a role in these changes.

The continental configuration of the world during the Miocene was similar to the present. However, plate tectonics led to intense palaeogeographical changes around the world during the Miocene, especially the Early and Middle Miocene. These changes contributed to fluctuations in the Neogene climate, in particular the opening of some ocean gateways (Drake Passage, Bering Strait) and the closure of others (the Atlantic-Pacific passage across Panama, the passage between the Indian Ocean and the Tethys) (Pagani *et al.* 2000; Hall *et al.* 2003). Changes in oceanic circulation at that time led to the establishment of the modern ocean circulation pattern (e.g. the Antarctic Circumpolar Current) that in turn affected the global climate. Ocean general circulation model simulations have shown the influence of ocean on global climate through changes in oceanic heat transport (e.g. Nisancioglu *et al.* 2003; Mikolajewicz *et al.* 1993). In addition, many atmospheric general circulation model (GCM) simulations have shown the influence of the uplift of mountain ranges and plateaus (Rocky Mountains, Andes, Himalayas, Alps, Tibetan Plateau) on global climate through changes in the atmospheric circulation (e.g. Ruddiman & Kutzbach 1989; Kutzbach *et al.* 1993; Ramstein *et al.* 1997; Fluteau *et al.* 1999; Kutzbach & Behling 2004).

Other authors have demonstrated that the Miocene climate variability was driven by fluctuations in the amplitude of obliquity and eccentricity (Westerhold *et al.* 2005). DeConto & Pollard (2003a, b) argue for a combination of atmospheric CO₂, orbital forcing and ice-climate feedbacks as the primary causes of climate transitions. Recently, Moran *et al.* (2006) have shown the dominance of greenhouse gases on climate control over tectonic forcing. The vegetation also had a significant influence on the Neogene climate. Climate model experiments demonstrate that the presence of high-latitude forests caused a warming in polar regions in the Miocene and, therefore, contributed to a weaker-than-present equator-to-pole temperature gradient (Dutton and Barron 1997; Micheels *et al.* unpublished data). Palaeovegetation changes, such as the evolution of grasslands during the Neogene (Retallack 2001), have an influence on the climate and must be considered when attempting to explain climatic fluctuations.

For Western European and Mediterranean regions, the Neogene vegetation history is well known as many

pollen sequences have been studied during the last few decades. At present, more than 120 pollen records from the Early Miocene to the Early Pleistocene are available in this area (Zagwijn 1960; Suc 1980; Diniz 1984a, b; Bessedik 1985; Zheng 1986; Bertini 1992; 1994; 2001, 2003; Clet-Pellerin 1996; Bertini & Roiron, 1997; Bachiri-Taoufiq 2000; 2003; Jiménez-Moreno 2005), providing a reliable and accurate view of latitudinal and altitudinal vegetation change (Suc 1989; Suc *et al.* 1995a, b; Jiménez-Moreno & Suc 2007). The pollen-based descriptions of the palaeovegetation are supported by a number of macrofossils studies (Kovar-Eder *et al.* 2006).

In this paper, we reconstruct the evolution of climatic gradients in Europe and the Mediterranean region during the Neogene based on pollen data for four periods: the Middle Miocene, around 14 million years (Ma); the Late Miocene around 10 Ma (Tortonian); the Early Pliocene, around 5–5.3 Ma; and the Middle Pliocene, around 3.5 Ma. For each time-slice, the vegetation is briefly described based on the pollen records.

Methodology for climate reconstruction from pollen data

In order to produce comparable and homogenous results, the same transfer function was applied to all selected pollen sequences. The climate was estimated using the 'Climatic Amplitude Method' developed by Fauquette *et al.* (1998a, b) to quantify the climate of periods for which no modern analogues of the pollen spectra exist. The Neogene spectra contain a mixture of temperate, warm-temperate and subtropical plants (even tropical plants during the Miocene) that today live in different parts of the world. The past climate is estimated by transposing the climatic requirements of the maximum number of modern taxa to the fossil data. This method may be applied to the Neogene period as the pollen flora of the region has been defined following botanical nomenclature for many years now (Zagwijn 1960; Pons 1964; Elhai 1969; Suc 1976; Diniz 1984a, b; Bessedik 1985).

In contrast to other methods such as the best analogue method (Guiot 1990), this approach does not rely on the analysis of entire pollen assemblages, but on the relationship between the relative pollen abundance of each individual taxa and the climate. Presence/absence limits, as well as abundance thresholds, have been defined for 60 taxa from modern pollen spectra and the literature. This method takes into account not only the presence/absence criterion but also pollen percentages to provide more reliable reconstruction. Low abundances of some tropical and subtropical taxa

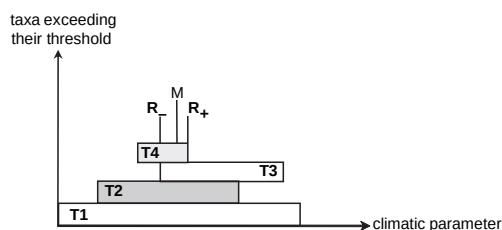


Fig. 1. Principle of the 'Climatic Amplitude Method' (Fauquette *et al.* 1998a, b). The most probable climate for a set of taxa exceeding their presence/absence and/or abundance thresholds in a pollen spectrum corresponds to the smallest climatic interval suitable for a maximum number of taxa [R-; R+]. A 'most likely value' (M) is then calculated (see text).

(e.g. *Microtropis fallax*, *Avicennia*) are meaningful and should be taken into account as these plants produce relatively small numbers of pollen grains. Conversely, low abundances of wind-pollinated taxa (e.g. *Quercus*, *Alnus*, *Corylus*) may reflect long-distance transport of these high pollen producers by air and water. In this case, very low pollen percentages are not significant.

With this method, the most probable climate for a fossil pollen assemblage is estimated as the climatic interval in which the highest number of taxa can exist (Fig. 1). The climatic estimate is presented as an interval [R-; R+] and as a 'most likely value' (M), which corresponds to a mean that is weighted according to the size of the climatic intervals of all taxa exceeding their presence/absence and/or abundance thresholds. As the precision of the information obtained from a taxon's climatic interval is inversely related to the breadth of this interval, the weights are greater for taxa with smaller intervals.

In this paper, we present reconstructions of two climatic parameters estimated from the pollen data: the mean annual temperature (Ta) and the mean annual precipitation (Pa).

High latitude/altitude taxa were excluded from the reconstruction process. The identification and exclusion of high latitude/altitude plants is based on numerous palynological studies (e.g. Suc *et al.* 1995a, b, 1999; Jiménez-Moreno, 2005) that show the Neogene vegetation zonation to follow a similar latitudinal and altitudinal zonation to that observed in present-day south-eastern China (Wang 1961), where most of the taxa that had disappeared from Europe by the late Neogene may be found. The estimates obtained, therefore, correspond to the climate at low to middle-low altitude (Fauquette *et al.* 1998a).

Pinus and non-identified Pinaceae (due to poor preservation of these disaccate pollen grains) have been excluded from the pollen sum of the fossil

spectra (Fauquette *et al.* 1998a, 1999). The pollen grains of these taxa are often over-represented in the sediments due to their high production and over-abundance in air and water (fluvial and marine) transport (Heusser 1988; Cambon *et al.* 1997).

The climatic latitudinal gradient during the Middle Miocene (c. 14–15 Ma)

A number of new pollen samples covering this period have recently been published (Jiménez-Moreno 2005). The samples are located along a latitudinal range in western Europe, from 47° to 36° N. The Mid-Miocene palaeogeography, which is now well established (Rögl 1998; Meulenkaamp & Sissingh 2003; Goncharova *et al.* 2004; Ilyna *et al.* 2004; Paramonova *et al.* 2004) has shown that these sites were (a) separated by around 12° in latitude at that time (instead of 11° today) and (b) situated a few degrees further south than today (Rögl 1998).

The study sites are (from north to south): Le Locle outcrop (western Switzerland), Les Mées borehole (southern France), Bayanne outcrop (southern France), Farinole outcrop (Corsica, France), La Rierussa outcrop (northeastern Spain), Gor outcrop (southern Spain), Alborán A-1 borehole (southern Spain), Andalucía G-1 borehole (southern Spain) (Fig. 2). Le Locle locality is dated from the upper mammal unit MN16 (Kälin *et al.* 2001). The other sites are marine deposits and are generally dated by micropalaeontology: Gor: calcareous nannofossil Zone CN-3 (Martín-Pérez & Viseras 1994); the time-interval taken from the Andalucía G1 borehole has been dated by planktonic foraminifera and ranges from zones N10 to N16 (Calandra in ELF 1984); the time-interval taken from the Alborán A1 borehole has been dated by planktonic foraminifera and ranges from zones N10 to N14 (Bailey *et al.* in CHEVRON 1986); La Rierussa: planktonic foraminifera (zone N4: Magné 1978) and calcareous nannofossil (zone NN4: C. Müller in Bessedik 1985); Farinole: planktonic foraminifera (zone N10) and calcareous nannofossils (zone NN6) (Ferrandini *et al.* 1998); Bayanne: planktonic foraminifera (zones N7 and N8: Besson *et al.* 2005). The Les Mées 1 borehole samples contain no micropalaeontological information. These samples have been allocated to the late Burdigalian as they correspond to the transgressive maximum according to the regional stratigraphy (Dubois & Curnelle 1978). Complete information is available in Jiménez-Moreno (2005).

Pollen taxa have been grouped following Suc (1989) and are detailed in Table 1.

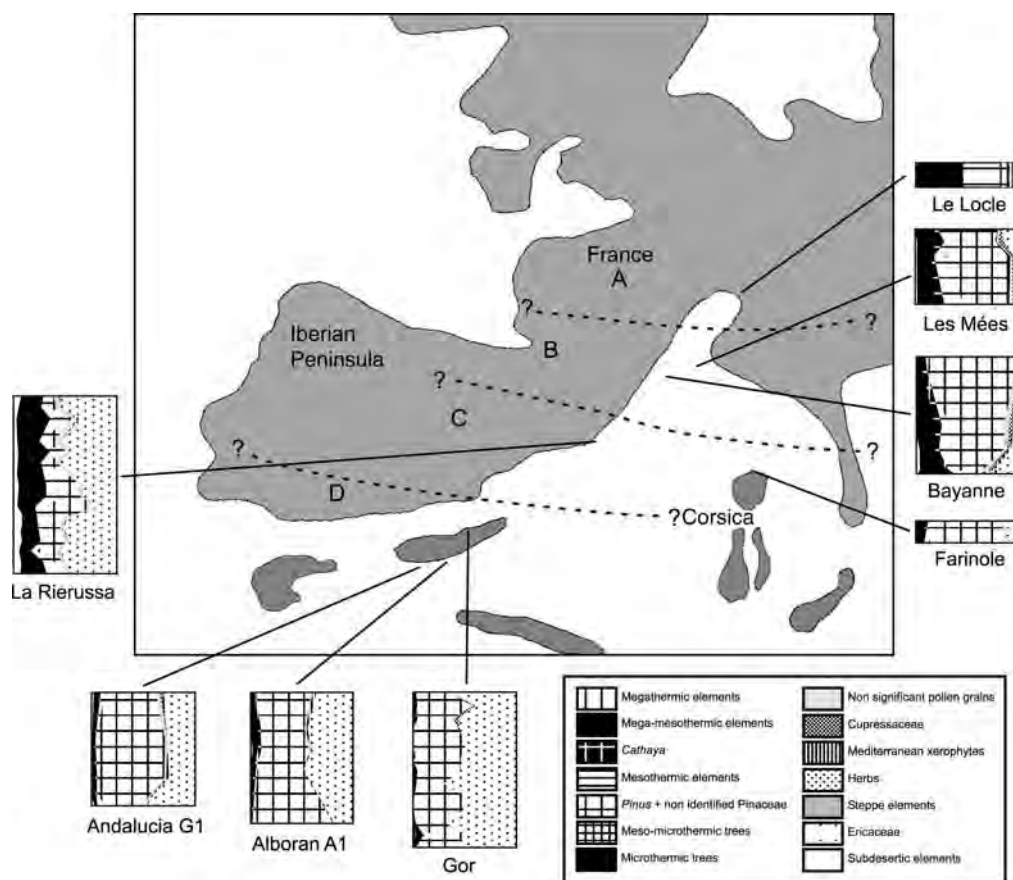


Fig. 2. Location of the studied sites covering the Middle Miocene and their synthetic pollen diagrams in the palaeogeographical framework of the early Serravallian (from Rögl 1998). Pollen localities (Jiménez-Moreno 2005): Le Locle-Combe Girard, Les Mées, Bayanne, La Rierussa, Farinole, Gor, Alborán A1, Andalusia G1. The four vegetational regions reconstructed from pollen data are indicated (A, B, C, D, see text for explanation).

The studied area can be subdivided into four vegetational domains from north to south on the basis of the pollen floras (Fig. 2) (Jiménez-Moreno 2005; Jiménez-Moreno & Suc 2007):

- In Western Switzerland (Fig. 2, zone A), the pollen flora is characterized by a high abundance of mega-mesothermic (= subtropical) elements, in particular *Taxodium* type and *Engelhardia*, and by high percentages of mesothermic (= warm-temperate) elements (mainly *Quercus* deciduous type). Some megathermic (= tropical) elements are present at low abundances. Percentages of herbs are very low.
- Southern France (Fig. 2, zone B) is characterized by the dominance of mega-mesothermic elements as well as temperate elements. *Avicennia*, a mangrove plant, is regularly present.

Herbaceous percentages are higher, but do not dominate the pollen spectra. Semiarid taxa such as *Acacia*, *Caesalpiniaceae* or *Prosopis* are recorded at very low values.

- In northeastern Spain and Corsica (Fig. 2, zone C), pollen spectra are rich in herbs and shrubs. *Caesalpiniaceae* and *Acacia* occur at very low percentages in the pollen spectra. Mega-mesothermic and mesothermic taxa are highly abundant. Megathermic elements are abundant in all the samples. *Avicennia* plays an important role in this area, indicating the presence of an impoverished mangrove along the coast. Meso-microthermic and microthermic taxa (i.e. inhabiting middle and high altitudes, respectively), including *Cathaya*, a conifer living today in the subtropical mid-altitude forests of southern China (Wang 1961), occur infrequently in these samples.

Table 1. *Taxa groups*

Megathermic elements	Rutaceae, <i>Mussaenda</i> type, Acanthaceae, <i>Acacia</i> , <i>Sindora</i> , <i>Croton</i> , <i>Alchornea</i> , <i>Bombax</i> , <i>Buxus bahamensis</i> type, <i>Mappianthus</i> , Rubiaceae, Euphorbiaceae, <i>Avicennia</i> , <i>Phyllanthus</i> type, Melastomataceae, Simarubaceae
Mega-mesothermic elements	<i>Symplocos</i> , <i>Engelhardia</i> , Sapotaceae, <i>Platycarya</i> , <i>Distylium</i> , <i>Rhoiptelea</i> , Taxodiaceae, <i>Taxodium</i> type, Hamamelidaceae, <i>Rhodoleia</i> , Lorantheaceae, <i>Microtropis fallax</i> , <i>Embolanthera</i> , <i>Corylopsis</i> , <i>Mallotus</i> , Celastraceae, <i>Parthenocissus</i> , <i>Leea</i> , <i>Myrica</i> , Menispermaceae, Theaceae, <i>Aesculus</i>
Mesothermic elements	<i>Quercus</i> deciduous type, <i>Fagus</i> , <i>Ostrya</i> , <i>Carpinus</i> , <i>Carya</i> , <i>Pterocarya</i> , <i>Juglans</i> , <i>Juglans cathayensis</i> type, <i>Parrotia</i> cf <i>persica</i> , <i>Liquidambar</i> , <i>Tilia</i> , <i>Castanea-Castanopsis</i> type, <i>Parrotiopsis jacquemontiana</i> , Restionaceae, <i>Buxus sempervirens</i> , <i>Ilex</i> , <i>Eucommia</i> , <i>Ligustrum</i> , <i>Populus</i> , <i>Ulmus</i> , <i>Zelkova</i> , <i>Celtis</i> , <i>Elaeagnus</i>
Meso-microthermic elements	<i>Cedrus</i> , <i>Tsuga</i> , <i>Sciadopitys</i>
Microthermic elements	<i>Picea</i> , <i>Abies</i> , <i>Keteleeria</i>
Mediterranean xerophytes	<i>Quercus ilex-coccifera</i> type, <i>Olea</i> , <i>Phillyrea</i> , <i>Ceratonia</i> , Cistaceae, <i>Pistacia</i> , <i>Nerium</i>
Herbs	Poaceae, Asteraceae Asteroideae, Asteraceae Cichorioideae, Centaurea, Convolvulaceae, <i>Plantago</i> , Ericaceae, Brasicaceae, <i>Helianthemum</i> , Geraniaceae, <i>Erodium</i> , Caryophyllaceae ...
Steppe elements	<i>Artemisia</i> , <i>Ephedra</i>
Subdesertic elements	<i>Lygeum</i> , <i>Neurada</i> , <i>Calligonum</i> , <i>Nitraria</i> , <i>Prosopis</i> , Agavaceae

- Southern Spain (Fig. 2, zone D) is characterized by the dominance of herbs and shrubs in the pollen spectra; Poaceae and halophytes are repeatedly found at high values. Further, subdesertic elements, such as *Nitraria*, *Lygeum*, *Prosopis*, *Neurada* and *Calligonum* are very abundant. Significant amounts of megathermic elements, including *Avicennia*, occur in all samples. Mega-mesothermic and mesothermic are regularly present. Meso-microthermic and microthermic elements appear sporadically at very low values. These pollen spectra with high percentages of herbs are typical of an open environment.

The presence, all along this transect, of plants characterized by high thermic requirements such as *Engelhardia*, *Myrica*, *Taxodium*-type, *Mussaenda*-type and *Avicennia*, indicates that the latitudinal temperature gradient was lower than today. This is consistent with the presence in other pollen data, covering the Mid-Miocene of Central Europe, of thermophilous taxa at high latitudes (Jiménez-Moreno 2005; Jiménez-Moreno & Suc 2007). The occurrence of thermophilous plants at higher latitudes has also been observed in North America by Liu & Leopold (1994). These authors estimated a thermic gradient of 0.3 °C per degree of latitude for North America (between 35° N–65° N) during the Mid-Miocene.

There are, however, important changes in the vegetation from north to south in Western Europe, occurring gradually between Switzerland and

southern Spain (between 36° N and 47° N). The vegetation becomes more and more open from north to south with the presence of subdesertic taxa in southern Spain, reflecting a latitudinal gradient in precipitation.

The results of the climatic quantification (Fig. 3) show, from north to south, increasing annual temperatures but decreasing annual precipitation. The reconstructed most likely values show higher mean annual temperatures than today all along the gradient (c. 2 to 8 °C higher) and higher mean annual precipitation than today in Southern France, Corsica and northeastern Spain (between 400 mm and 700 mm higher). In southwestern Europe, the mean annual precipitation is almost equivalent to modern values (maximum 200 mm higher). This is also the case at Le Locle, where little change in mean annual precipitation values is shown. The thermic gradient is weaker than the modern one as the differences between the Miocene and the modern temperatures are between c. 2 °C in southern Spain, c. 4 °C in northern Spain, c. 5/6 °C in southern France and c. 8 °C in western Switzerland. On the basis of the most likely value reconstructed from pollen data, the thermic gradient in Western Europe was around 0.48 °C per degree in latitude whereas it is around 0.6 °C today (Ozenda 1989). This result is in agreement with the estimations obtained by Bruch *et al.* (2004) from fossil floras of Europe where they find a lower latitudinal temperature gradient than today.

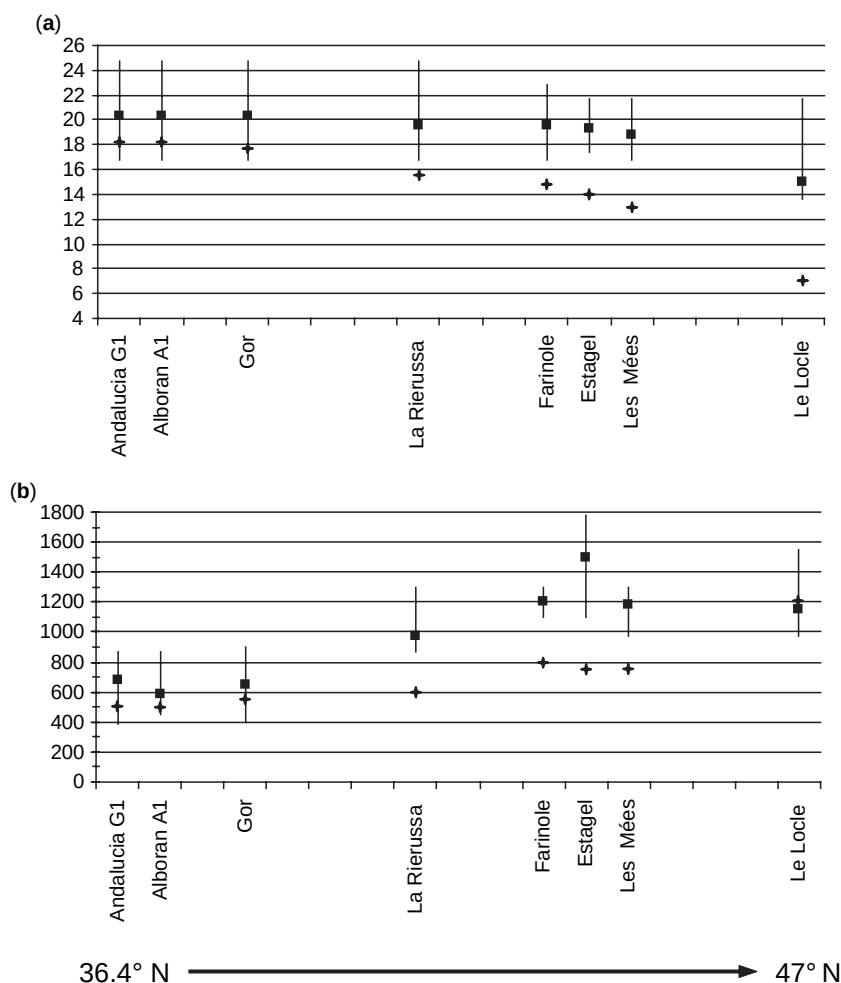


Fig. 3. Climatic reconstruction from pollen data (climatic interval and most likely value) in Western Europe and Mediterranean region showing (a) the gradient of temperature (mean annual temperature in °C) and (b) precipitation (mean annual precipitation in mm) for the Middle Miocene. Modern values are indicated by a cross to show the differences between modern and Miocene latitudinal gradients. Pollen data of Le Locle-Combe Girard, Les Mées, Bayanne, La Rierussa, Farinole, Gor, Alborán A-1, Andalusia G-1 (Jiménez-Moreno 2005) have been used.

The latitudinal climatic gradient at the end of the Miocene (Tortonian, *c.* 10 Ma)

For this period, pollen spectra from the sites of Ambérieu (Farjanel & Mein 1984), Mirabel (Naud & Suc 1975), Sanabastre and Sampsor in Cerdanya (Bessedik 1985), Zaratan (Rivas-Carballo *et al.* 1994), Capodarso in Sicily (Suc *et al.* 1995c) and MSD 1 borehole in Morocco (Bachiri-Taoufik 2000) have been used to estimate the climatic gradient (Fig. 4). The palaeogeography has been established by Paramonova *et al.* (2004). The Cerdanya

sites (Agusti & Roca 1987), Zaratan (Rivas-Carballo *et al.* 1994) and Ambérieu (Farjanel & Mein 1984) were assigned to the Tortonian on the basis of mammal biochronology. The site of Mirabel belongs to the volcanic Coirons area and has a radiometric age (Naud & Suc 1975). Planktonic foraminifera are available for the MSD1 borehole for zones N16 and N17 (Barhoun 2000). The Capodarso section covers the late Tortonian to early Messinian according to planktonic foraminifera and calcareous nannofossils (Cita *et al.* 1973; Suc *et al.* 1995c). Only the lower part of this section is considered here.

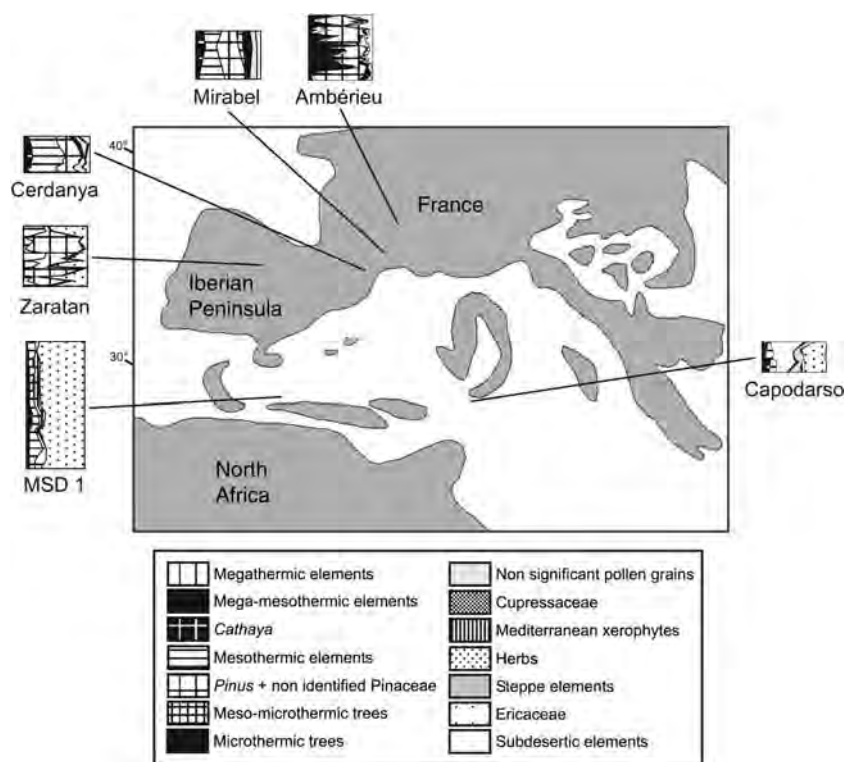


Fig. 4. Location of the studied sites covering the Tortonian around 10 Ma in Western Europe and Western Mediterranean region and their synthetic pollen diagrams in the palaeogeographical framework of the Late Tortonian (Paramonova *et al.* 2004). Pollen localities: Ambérieu (Farjanel and Mein 1984), Mirabel (Naud & Suc 1975), Sanabastre and Sampsor sites in Cerdanya (Bessedik 1985), Zaratan (Rivas-Carballo *et al.* 1994), Capodarso in Sicily (Suc *et al.* 1995c) and MSD 1 borehole in Morocco (Bachiri-Taoufiq 2000).

Although less pollen data exist for this period, a clear latitudinal gradient is observed for both temperature and precipitation. In northwestern Europe (Ambérieu, Mirabel sites), pollen data indicate forested environments, characterized by taxa growing under a wet climate (*Taxodiaceae*, *Engelhardia*, *Symplocos*, *Platycarya*...). Forested environments are also indicated in the northwestern Mediterranean region (Sanabastre/Sampsor sites in Cerdanya, Bessedik 1985), where arboreal pollen dominates with low values of herbaceous taxa. The microflora is characterized by the dominance of *Quercus*, *Fagus*, *Alnus* and conifers (*Cathaya*, *Pinus*, *Taxodiaceae*), reflecting the presence of mixed deciduous forests. Pollen grains of *Abies* are also recorded. Only few megathermic plants are present at low values. However, the presence, in the Cerdanya Basin, of plants such as evergreen *Quercus* (in the microflora) or even *Cassia*, *Mahonia*, *Cinnamomum*, *Banksia*, *Combretaceae* (in the macroflora, Menendez Amor 1955) indicates a warmer climate than today. At Zaratan, the pollen

assemblages are similar to those found today in the southwestern Mediterranean region with sclerophyllous woods of *Quercus* and pines associated with species characteristic of open vegetation as *Cistaceae*, *Cupressaceae*, *Ericaceae*, *Geraniaceae* and *Plantago*. The presence of deciduous taxa indicates a warm-temperate climate in this region (Rivas-Carballo *et al.* 1994). Finally, in the southwestern Mediterranean region (Capodarso in Sicily and MSD 1 borehole in Morocco), the pollen spectra are largely dominated by herbaceous taxa, indicating dry open environments with the presence of subdesertic herbs such as *Lygeum*. However, pollen data also indicate the presence of forests on the surrounding uplands. The record of *Avicennia* in the MSD 1 borehole (Bachiri-Taoufiq 2000) indicates an impoverished mangrove along the south Mediterranean shoreline during the Tortonian.

The climatic reconstruction based on these pollen sequences shows that temperatures were higher than today during the Tortonian, in particular in the northwestern Mediterranean area. The climate

was warm and humid in Western Europe (most likely values 4 to 9 °C and annual precipitation rainfall 100 to 600 mm higher than today), and warm and dry in the south Mediterranean region (most likely values of 3 to 4 °C higher and less than 200 mm higher than today). The difference between the Tortonian and the modern annual temperature is larger for the site of Sampson. Indeed, this site is currently situated at about 1000 m above sea level but was at lower altitude during the Tortonian (Mauffret *et al.* 2001).

The climatic estimates show that the north–south climatic gradient that existed during the Tortonian was similar to today, with increasing temperature and decreasing precipitation, but with

higher temperatures (Fig. 5). On the basis of the most likely values reconstructed from pollen data of MSD 1 borehole and Ambérieu section, the thermic gradient is around 0.6 °C per degree in latitude. This does not agree with the estimated reduction of about 50% in the thermic gradient calculated by Bruch *et al.* (2006) from fossil floras of Central and Eastern Europe.

The climatic latitudinal gradient for the Early Pliocene (c. 5.0–5.3 Ma)

During this period, the palaeogeography was similar to today, with the exception of the existence

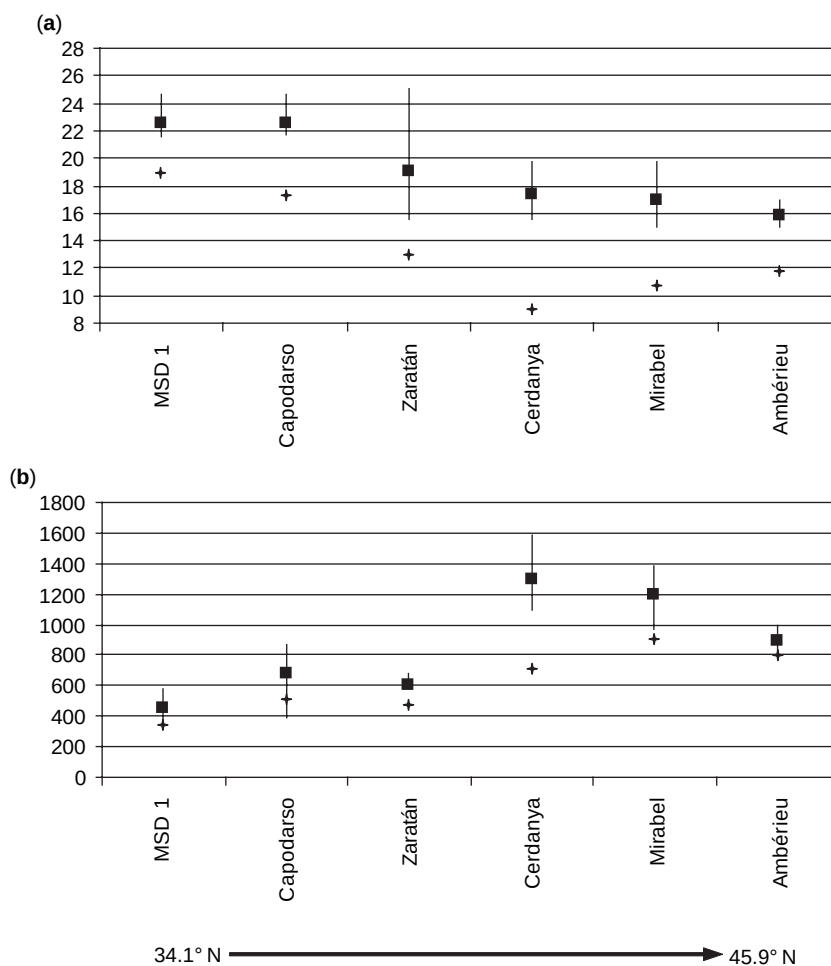


Fig. 5. Climatic reconstruction (climatic interval and most likely value) from pollen data covering the Tortonian in Western Europe and the Mediterranean region showing (a) the temperature gradient (mean annual temperature in °C) and (b) the precipitation gradient (mean annual precipitation in mm). Modern values are indicated by a cross.

of rias (corresponding to the excision of deep canyons by rivers during the desiccation of the Mediterranean Sea margins at the time of the Messinian Salinity Crisis), which penetrated lands (Clauzon *et al.* 1995). During the earliest part of the Pliocene (5.33 Ma), the reflooding of the Mediterranean basin by Atlantic waters (to about 70–80 m above the present-day sea level, Haq *et al.* 1987) resulted in the accumulation of terrigenous sediments in a large number of areas. As a result, this period is rich in pollen sites. Here, we have used pollen spectra from the sites of Susteren 752/72 (Zagwijn 1960), Stirone (Bertini 1994, 2001), Saint-Martin du Var (Zheng 1986), Cap d'Agde 1 (Suc 1989), Le Boulou (Suc *et al.* 1999), Garraf 1 (Suc & Cravatte 1982), Tarragone E2 (Bessais & Cravatte 1988), Rio Maior F16 (Diniz 1984a, b), Capo Rossello (Suc *et al.* 1995c), Andalucia G1 (Suc *et al.* 1995a), Oued Tellil (Suc *et al.* 1999), Nador 1 (Fauquette *et al.* 1999), Habibas 1 (Suc *et al.* 1999), to estimate the climatic gradient during the Early Pliocene. All sites (except Susteren and Rio Maior F16) are marine deposits belonging to the Mediterranean earliest Pliocene and are well-dated by both planktonic foraminifera (zones MP11-3) and calcareous nannofossils (zones NN12-13) (Suc *et al.* 1995b). In addition, the lowermost layers of these sequences directly overlie the Messinian erosional surface, providing a synchronous chronological marker at 5.33 Ma (Clauzon *et al.* 1996). The lower part of the Susteren borehole belongs to the Brunsumian climatic phase (Zagwijn 1960). The lower part of the Rio Maior F16 borehole has been correlated to the Brunsumian climatic phase on the basis of a similar evolution of the vegetation to the Early Pliocene changes recorded in the Garraf 1 borehole (Suc & Zagwijn 1983; Suc *et al.* 1995b).

Three main vegetation domains in Western Europe and the Mediterranean region (Fig. 6) have been described by Suc (1989) and Suc *et al.* (1995a), during the Early Pliocene, with a clear latitudinal zonation of vegetation. Sites on the Atlantic coast of Western Europe (Fig. 6, zone A, Susteren and Rio Maior sites) show forested vegetation dominated by Taxodiaceae, Ericaceae and mesothermic deciduous trees (*Quercus*, *Carya*, *Pterocarya*, *Acer*, *Carpinus*, *Fagus*, *Liquidambar*, *Parrotia persica*). In the north Mediterranean region (Fig. 6, zone B), the forests were dominated by Taxodiaceae (*Taxodium*/*Glyptostrobus* or *Sequoia* dependent on local environment conditions, respectively swamps and slopes), accompanied by mega-mesothermic plants such as *Engelhardia*, *Symplocos* and *Platycarya*. These latter taxa were reduced later, in the Mid-Pliocene. The South Mediterranean region (Fig. 6, zone C) was characterized by Mediterranean xerophytic

ecosystems ('matorral' composed by *Olea*, *Phillyrea*, *Pistacia*, *Ceratonia*, evergreen *Quercus*, *Nerium*, *Cistus*) and, to the south, by open environments dominated by subdesertic plants like *Lygeum*, *Neurada*, *Nitraria*, *Calligonum*, Geraniaceae and Agavaceae.

The climatic reconstruction shows that temperatures at the beginning of the Pliocene at around 5.0–5.33 Ma were higher than today, particularly in the northwestern Mediterranean area. The average climate was warm and humid in Europe and the north Mediterranean region (most likely values 1 to 4 °C and precipitation 400 to 700 mm higher than today), and warm and dry in the south Mediterranean region (most likely values equal to or 5 °C higher and drier than or equal to today) (Fauquette *et al.* 1998b, 1999; Fauquette & Bertini 2003; this study). A north–south climatic gradient existed at the beginning of the Pliocene, with, as today, increasing temperatures and decreasing precipitation (Fig. 7). The thermic gradient calculated on the 'most likely values' of mean annual temperatures of Susteren and Habibas sites is around 0.65 °C per degree in latitude.

The climatic gradient reconstructed for the West European Pliocene, both for temperatures and precipitation, seems to be very similar to that observed today in northwestern North America and in particular in western California and Lower California. This gradient may be summarized as follows. The climate of northern California is particularly humid, with annual precipitation from c. 1000 to more than 2000 mm, especially in the Coast Ranges to the north of San Francisco (summer is the drier season). Mean annual temperatures range from 9 °C to 14 °C. To the south, in central California, the climate is less humid with precipitation ranging from c. 600 to 1500 mm/year. This region is characterized by decreasing humidity and an increasing summer drought from north to south. Mean annual temperatures are between 10 and 18 °C. In southern California, mean annual temperatures are between 14 and 24 °C and mean annual precipitation between 400 and 800 mm. Finally, in Lower California, the climate is arid with annual precipitation from c. 100 to 500 mm (Walter 1979; Thompson *et al.* 1999). Mean annual temperatures are comprised between 17 and 30 °C.

The vegetation zonation imposed by the latitudinal/altitudinal climatic gradients in this region is also similar to that of the European and Mediterranean Pliocene (Fig. 8). Humidity, as either rainfall or fog, allows the installation of dense *Sequoia* forests in Northern California in the littoral plain as well as in the Coast Ranges (Quézel & Barbero 1989; Thompson *et al.* 1999). These forests occur at up to 900 m a.s.l. on the

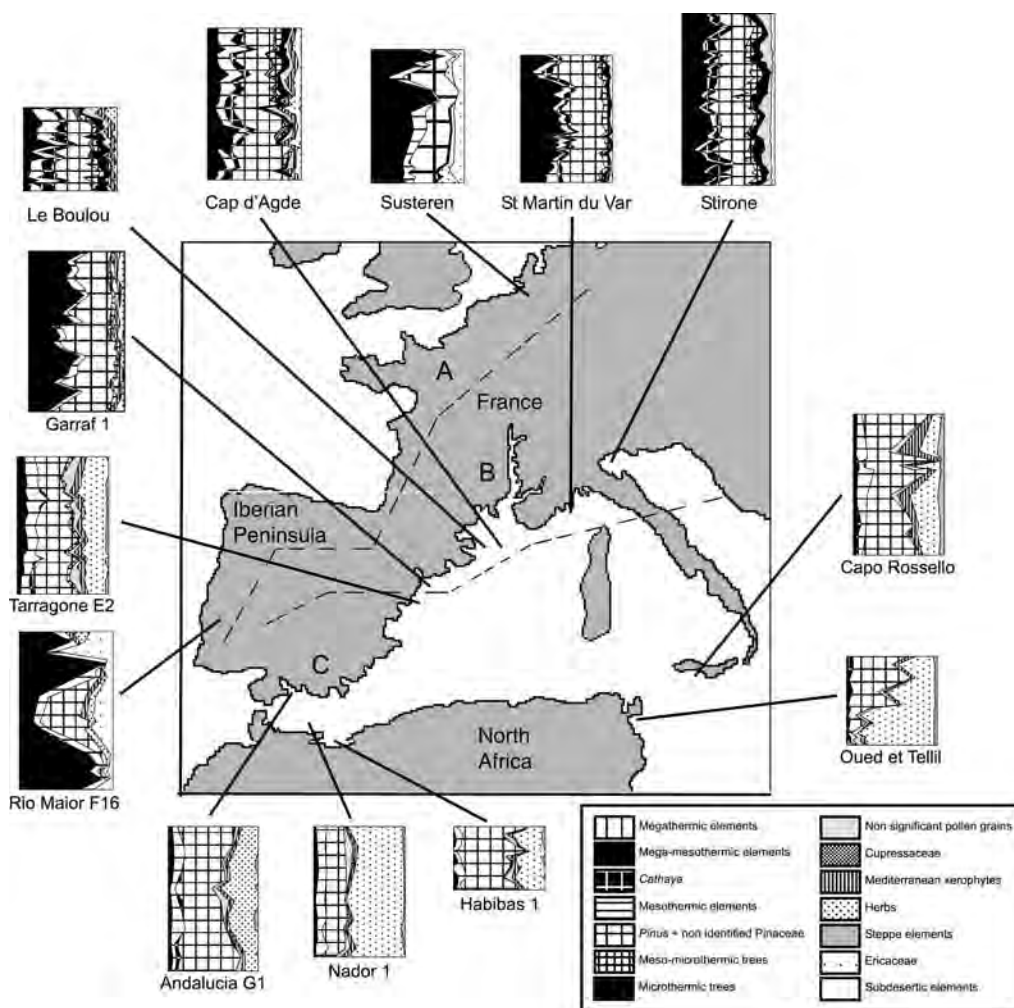


Fig. 6. Location of the studied sites covering the Early Pliocene, at around 5–5.3 Ma, and their synthetic pollen diagrams in the palaeogeographical framework of the Early Pliocene (Clauzon *et al.* 1995; Clauzon 1996; Jolivet *et al.* 2006). Pollen localities: Susteren 752/72 (Zagwijn 1960), Saint-Martin du Var (Zheng 1985), Stirone (Bertini 1994, 2001), Cap d'Agde 1 (Suc 1989), Rio Maior F16 (Diniz 1984), Andalucia G1 (Suc *et al.* 1995a), Le Boulou (Suc *et al.* 1999), Nador 1 (Fauquette *et al.* 1999), Habibas 1 (Suc *et al.* 1999), Tarragone E2 (Bessais & Cravatte 1988), Garraf 1 (Suc & Cravatte 1982), Oued et Tellil (Suc *et al.* 1999), Capo Rossello (Suc *et al.* 1995c).

Coast Ranges to the north of San Francisco. To the south, the occurrence of sequoias in the uplands becomes sparse (Quézel & Barbero 1989). This vegetation zone closely resembles the Europe and northwestern Mediterranean area dominated by Taxodiaceae and other taxa growing under a wet climate during the Early Pliocene.

Central and southern California are dominated by the chaparral vegetation type (Walter 1979), which resembles the Mediterranean 'matorral' *s.s.* defined by Quézel & Barbero (1989). This vegetation type developed in Europe during the Pliocene

with the appearance of the summer drought (Axelrod 1973; Thompson 1991; Thompson & Fleming 1996). The very low precipitation in Lower California prevents the installation of forests, and only a subtropical desert vegetation type may develop in this arid zone (Walter 1979). This zone may be compared to the subdesertic vegetation reconstructed for the Pliocene in North Africa (Suc *et al.* 1995b; Fauquette *et al.* 1999).

In California, therefore, the vegetation zonation imposed by the latitudinal climatic gradient along the Pacific coast shows very strong similarities to

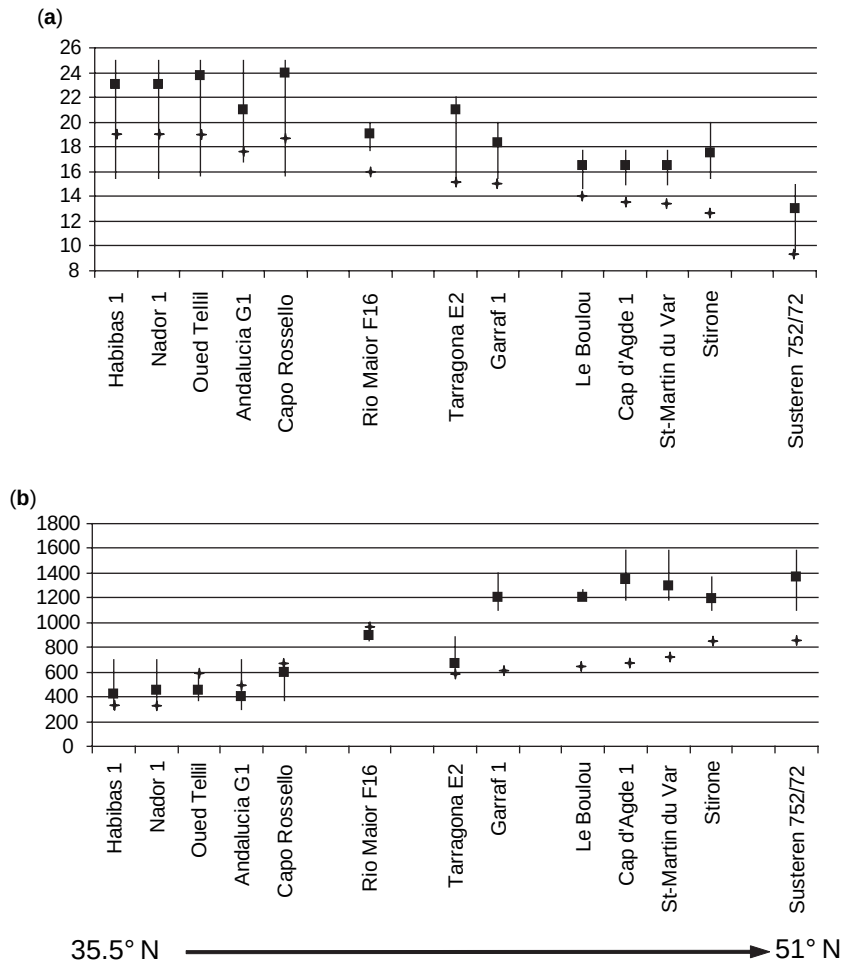


Fig. 7. Climatic reconstruction (climatic interval and most likely value) from pollen data covering the Early Pliocene (c. 5–5.3 Ma) in Western Europe and the Mediterranean region showing (a) the temperature gradient (mean annual temperature in °C) and (b) the precipitation gradient (mean annual precipitation in mm). Modern values are indicated by a cross.

the Pliocene in European and the Mediterranean region, with a development from dense humid forests in the north to subdesertic/desertic vegetation in the south. Changes in vegetation types to the north and south of the region considered also support this comparison. Today, the desertic zone is replaced to the south by intertropical forest in Central America (Walter 1979); a pollen sequence obtained from a borehole in the Guinea Gulf shows a similar change during the Pliocene in Central Africa, to the south of our study area (Suc *et al.* 1995b). In northern California, *Sequoia* forests are replaced to the north by forests

composed of *Tsuga* in association with other conifers and some deciduous trees such as *Alnus* (Walter 1979); during the Pliocene in Europe, *Tsuga* forests replaced *Sequoia* forests at higher altitudes and latitudes.

The climatic latitudinal gradient for the Middle Pliocene (c. 3.5 Ma)

The climatic gradient in Western Europe at around 3.5 Ma has been estimated using pollen spectra from the sites of Susteren (Zagwijn 1960),

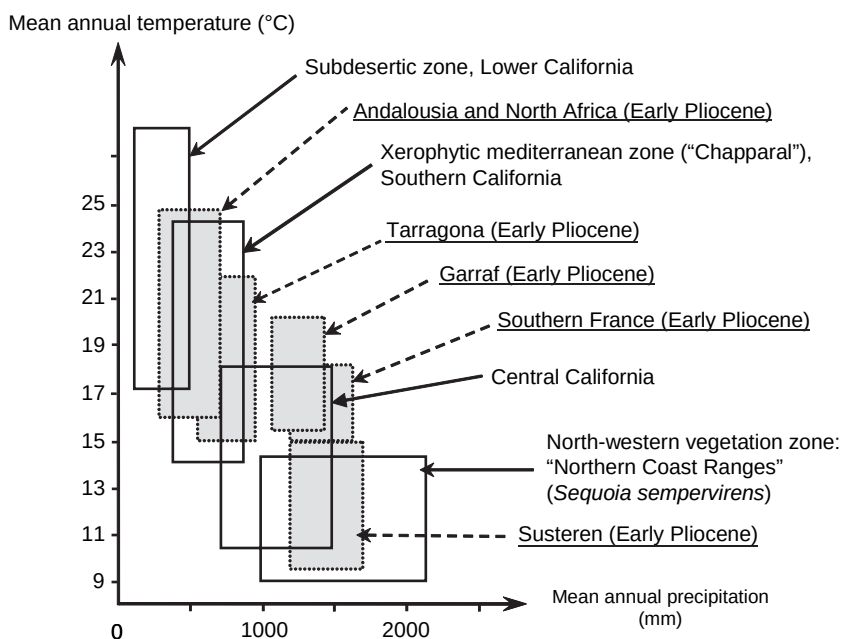


Fig. 8. Comparison between modern climate/vegetation structures of California and those of the Mediterranean Pliocene defined from pollen data and climate reconstruction.

La Londe (Clet & Huault 1987), Saint-Isidore (Zheng 1986), Garraf 1 (Suc & Cravatte 1982), Tarragona E2 (Bessais & Cravatte 1988), Andalucia G1 (Suc *et al.* 1995a), Habibas 1 (Suc *et al.* 1999) and Oued Galaa (Suc 1989) (Fig. 9). All sites, except Susteren, La Londe and Rio Maior F16, are marine deposits dated using planktonic foraminifera (zone MPI4): Saint-Isidore (Zheng & Cravatte 1986), Garraf 1 (Suc & Cravatte 1982), Tarragona E2 (Bessais & Cravatte 1988), Andalucia G1 (Suc *et al.* 1995b), Habibas 1 (J. Cravatte, unpublished information), Oued Galaa (J. Cravatte, unpublished information). The section of the Susteren borehole sequence used here belongs to the Reuverian climatic phase (Zagwijn 1960) and has been climatostratigraphically correlated to the upper part of the Rio Maior F16 pollen diagram (Suc *et al.* 1995b). The same method has been used to attribute uppermost part of the La Londe pollen diagram to the Praetiglian climatic phase (Clet & Huault 1987). The lower part of this section therefore belongs to the Reuverian climatic phase, correlated to the Mediterranean Piacenzian Stage (Suc & Zagwijn 1983; Suc *et al.* 1995b).

These pollen data show a clear climatic latitudinal gradient for both temperature and precipitation. In northwestern Europe, along the Atlantic coast (Fig. 9, zone A), the vegetation was characterized by taxa growing under a wet climate, as during

the Early Pliocene, but with a reduction in megamesothermic taxa (Suc *et al.* 1995a). In the northwestern Mediterranean region (Fig. 9, zone B), megamesothermic taxa are still well represented but there is a general increase in deciduous mesothermic taxa, especially at Saint-Isidore (southern France) where microthermic plants, which developed at higher altitudes, also increase. In the southwestern Mediterranean region (Fig. 9, zone C), pollen spectra have the same composition as those of the Early Pliocene, characterizing open steppe-like vegetation and dry and warm environments.

As during the Early Pliocene, the climate reconstructed from these pollen data show higher mean annual temperatures than today along the entire gradient (most likely values 3 to 6 °C higher than modern values) and mean annual precipitation that is higher than today in northwestern Europe (most likely values 400 to 700 mm higher), but equivalent to modern values in southwestern Europe (maximum 200 mm higher) (Fig. 10).

The difference in the climate reconstructions between the Early and Middle Pliocene is negligible despite notable variations in pollen assemblages between these two periods (e.g. decrease in pollen percentages of some megamesothermic trees but increase in pollen percentages of some mesothermic trees at Garraf in Catalonia, at Saint-Martin du Var and Saint-Isidore in southern France). These

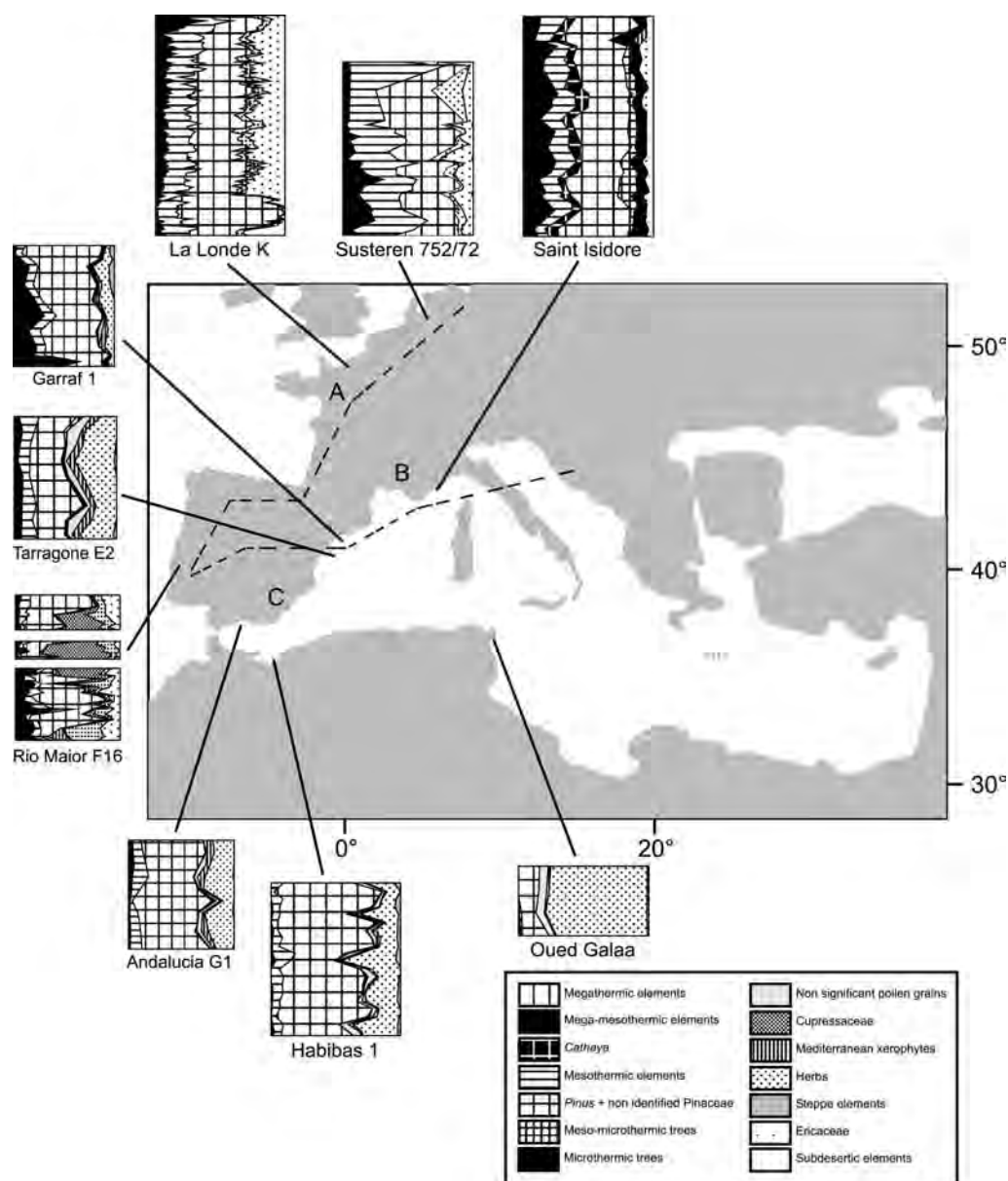


Fig. 9. Location of the studied sites covering the Middle Pliocene, at around 3.5–3 Ma in Western Europe and the Western Mediterranean region and their synthetic pollen diagrams in the palaeogeographical framework of the Middle Pliocene (Khondkarian *et al.* 2004). Pollen localities: Susteren 752/72 (Zagwijn 1960), La Londe (Clet & Huault 1987), Saint-Isidore du Var (Zheng 1985), Garraf 1 (Suc & Cravatte 1982), Tarragona E2 (Bessais & Cravatte 1988), Andalusia G1 (Suc *et al.* 1995a), Oued Galaa (Suc unpublished) and Rio Maior F16 (Diniz 1984).

variations in pollen records are often too slight to result in changes in the reconstructed climate. This result indicates the sensitivity limit of the 'Climatic Amplitude Method' and of all the methods based on the principle of co-existence intervals.

The West European climatic gradients during the Middle Pliocene, in particular the thermic gradient, appear to be very similar to that observed today, i.e. around 0.6 °C per degree in latitude (Fig. 10).

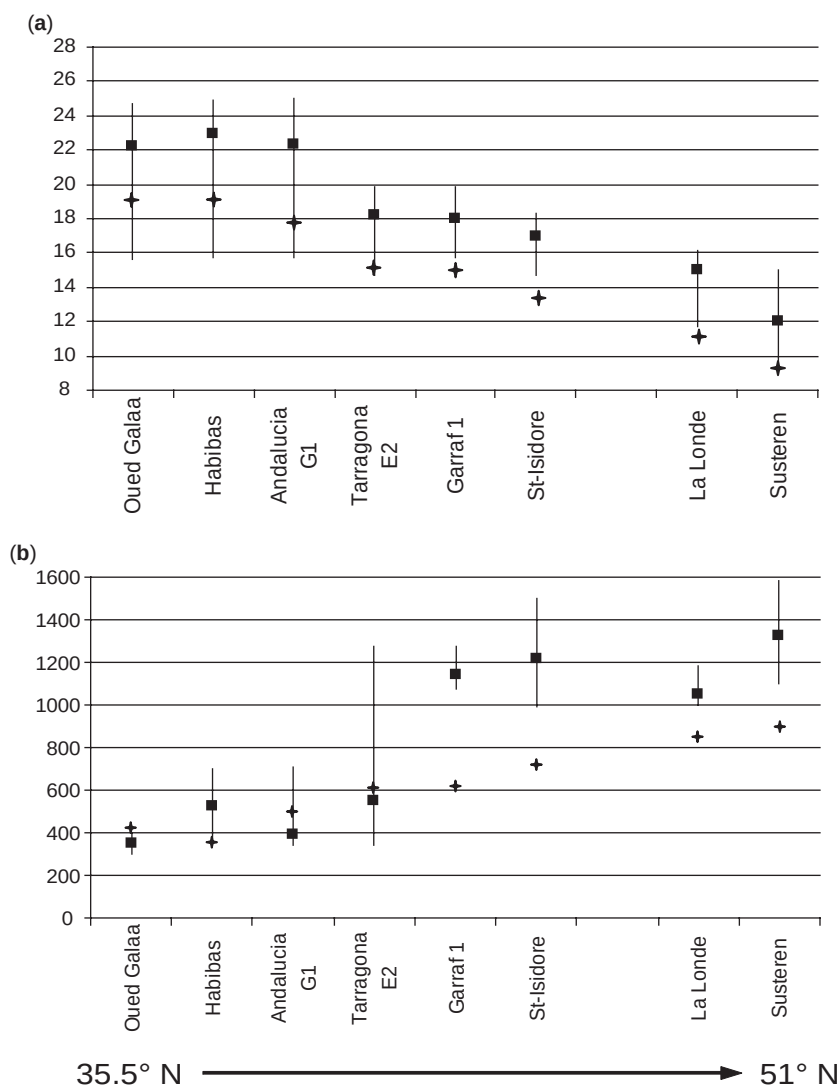


Fig. 10. Climatic reconstruction (climatic interval and most likely value) from pollen data covering the Middle Pliocene in Western Europe and Mediterranean region showing (a) the temperature gradient (mean annual temperature in °C) and (b) the precipitation gradient (mean annual precipitation in mm). Modern values are indicated by a cross.

Discussion

During the Middle Miocene, the reconstructed thermic gradient was approximately 0.48 °C per degree of latitude. Whilst this estimated value is certainly not the exact value as it is calculated using solely the most likely values, the weakening of the gradient is supported by changes in the entire climatic intervals. A weaker gradient during this period has also been suggested by other

studies based on macro- and microfloras of the circumalpine region and Central Europe (Bruch *et al.* 2004) and also in North America (Liu & Leopold 1994).

From the end of the Miocene (Tortonian) to the mid-Pliocene, the vegetation and climatic latitudinal gradients (in particular the thermic one) differ from those of the Middle Miocene. Temperatures were higher than today, as during the Mid-Miocene,

but the difference between the north and the south was greater than during the Mid-Miocene, resulting in a similar gradient in temperature and vegetation to today.

Our results place the transition, for mid-latitude regions, from the weak thermic gradient of the Mid-Miocene to the modern-like gradient of the Pliocene during the Middle–Late Miocene, before or during the Tortonian.

Simulations with the AGCM ECHAM4 coupled to a slab ocean model have been made in order to study the climate response during the Tortonian to a generally low palaeo-orography, a weaker-than-present palaeo-oceanic heat transport and a changed palaeovegetation (Steppuhn *et al.* 2006; Micheels *et al.* unpublished data). Climate trends in the Tortonian model simulations show an overall reduction of the meridional temperature gradient (Steppuhn *et al.* 2006; Micheels *et al.* unpublished data). For the Mediterranean region, the simulated climate is slightly warmer and drier than today (Micheels *et al.* unpublished data), which agrees with our data from southwestern Europe (Sicily, Central Spain). In northern Africa, the Tortonian model simulates warmer and less-arid conditions than today (Micheels *et al.* unpublished data). Our evidence for subdesertic herbs and forest elements in Morocco supports the climate modelling results. However, it should be noted that these two groups of plants certainly developed at different altitudes that may not be adequately resolved by the climatic model. The pollen flora of the Ambérieu and Mirabel sites indicate forest

environments that developed under a warm and wet climate. The Tortonian simulation indicates an increased precipitation over Central Europe. Although this simulation tends to be too cool at higher latitudes (Micheels *et al.* unpublished data), our data from Europe largely agree with the model simulation.

On the basis of fossil floras of Central and Eastern Europe, Bruch *et al.* (2006) indicate a much weaker thermic gradient than today during the Tortonian, with a reduction of approximately 50%. Whilst the ECHAM model is unable to reproduce this weak temperature gradient, our results show higher mean annual temperatures than the simulated zonal average temperature for land surfaces but agree with the thermic gradient simulated (Fig. 11).

Simulations have been made of the Mid-Pliocene climate by Haywood *et al.* (2000a) using the HadAM3 version of the UK Meteorological Office's (UKMO) general circulation model and by Jost (2005) using the LMDz (Laboratoire de Météorologie Dynamique, zoom, Institut Pierre Simon Laplace) atmospheric general circulation model.

Boundary conditions of the models are those established by the Pliocene Research, Interpretation and Synoptic Mapping group of the US Geological Survey (PRISM 2, see Cronin & Dowsett 1990; Dowsett *et al.* 1994, 1999). Jost (2005) confirms the increase in global temperatures compared to the present (Fig. 12a), previously shown by Haywood *et al.* (2000a). This increase is greater at mid- to high latitudes than at the equator.

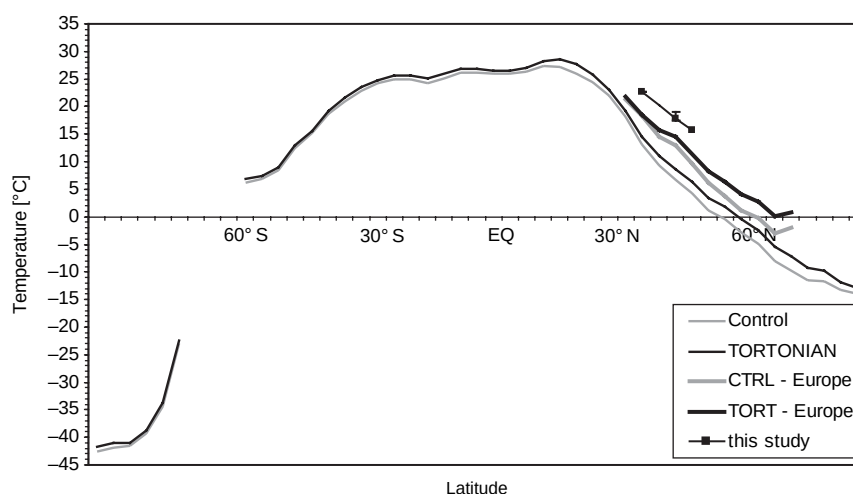


Fig. 11. The zonal average temperature (in °C) for land surfaces of the Tortonian simulation (black line), the present-day control simulation (grey line) and terrestrial proxy-data (squares and reconstructed interval). In order to obtain the zonal averages of proxy-data, the data locations are transformed into the grid point resolution (3.75°) of the model ECHAM4. For Europe, the zonal average temperatures of the model runs are shown separately.

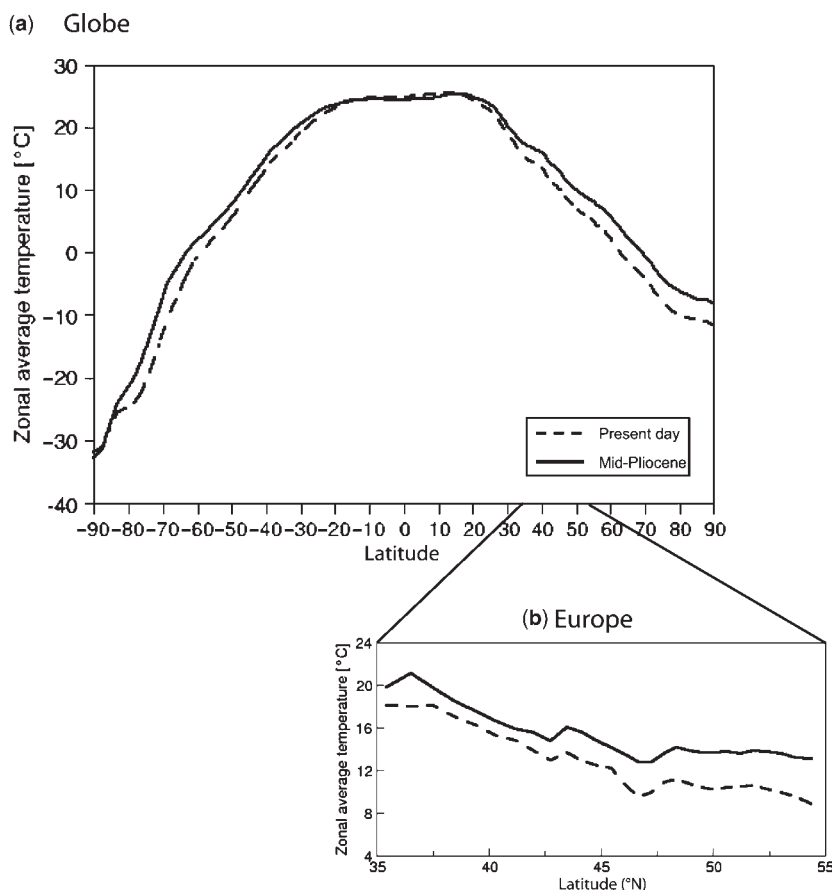
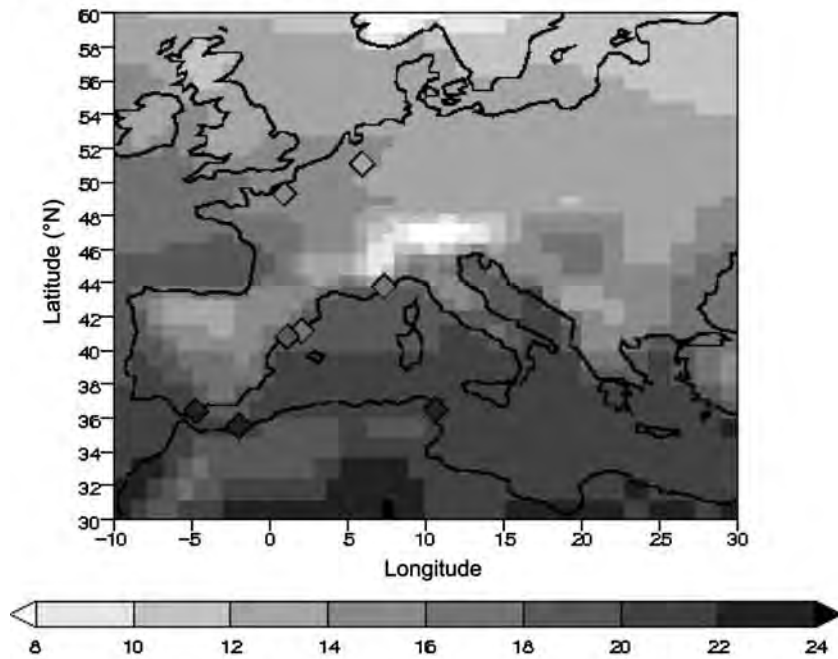


Fig. 12. The zonal average temperatures (in °C) for land surfaces of the Middle Pliocene simulation (bold line) and the present-day control simulation (dotted line), (a) for the globe, (b) for Europe (from -10 to 20° East and 35 to 55° West), from the LMDz AGCM (modified from Jost 2005).

However, despite this weakened pole-to-equator thermic gradient, the simulation shows similar changes of temperature at mid-latitudes of the Northern Hemisphere between the Middle Pliocene and today (Fig. 12b), suggesting that, for this region, the latitudinal thermic gradient was close to the modern one (i.e. around $0.6^{\circ}\text{C}/\text{degree}$ in latitude). This pattern is completely consistent with our reconstructed climate and vegetation distribution. The mean annual temperatures of the simulations cited above are in good agreement with the reconstructed climate (Fig. 13a) with temperatures that are clearly higher than today in the study region.

There are, however, some important differences between the reconstructed annual precipitation and changes simulated by the AGCM LMDz (Fig. 13b). Pollen data indicate in western Europe and in the western Mediterranean higher annual precipitation than the LMDz model.

On the contrary, the pollen-based precipitation estimates are in better agreement with the simulations by Haywood *et al.* (2000a, b). As shown on Figures 7 and 10, the precipitation gradient, whilst still decreasing from north to south, was more accentuated, with a larger difference between the Pliocene and today in the north than in the south. Haywood *et al.*'s simulations (2000b) show annual zonal average precipitation similar to modern values between around 30 and 42°N and higher than today between 42 and 51°N . This pattern is particularly true in Western Europe and western Mediterranean and has been explained by the authors by an increased arrival of southwestern air masses. During the Mid-Pliocene, the enhancement of the Icelandic low- and Azores high-pressure systems and the stronger pressure gradient in the North Atlantic caused an intensification of annual westerly wind strength. Combined

(a) Mean annual temperatures ($^{\circ}\text{C}$)

(b) Mean annual precipitation (mm)

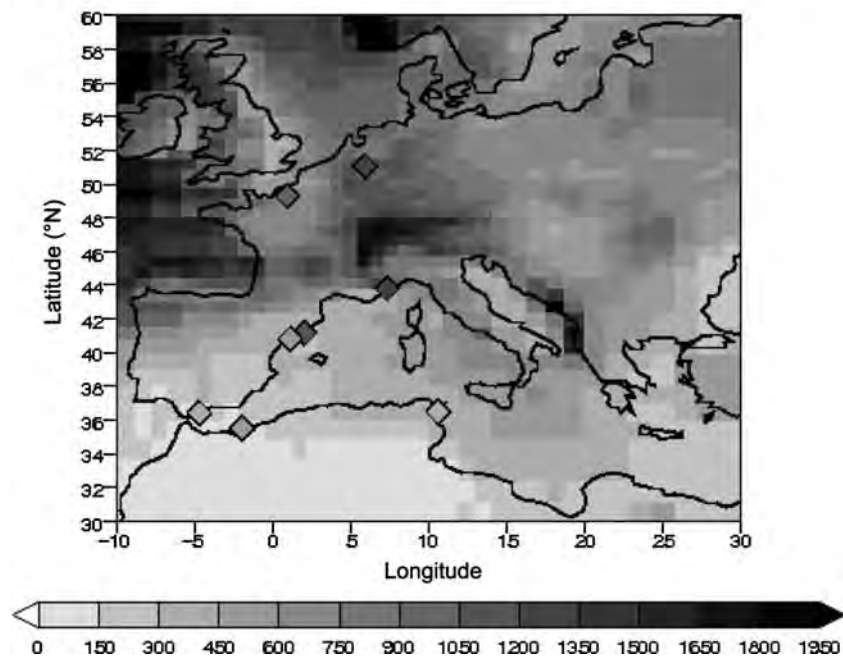


Fig. 13. Comparison for the Mid-Pliocene (3.5–3 Ma) between (a) mean annual temperatures and (b) annual precipitation simulated by the LMDz atmospheric general circulation model (modified from Jost 2005) and the values obtained from pollen data (diamonds).

with warmer sea-surface temperatures, the atmospheric transport of heat and moisture over Europe and the Mediterranean region was increased (Haywood *et al.* 2000a). This pattern is in agreement with the development of Ericaceae moors along the European Atlantic coast that suggest an enhanced westerly wind pattern (Suc *et al.* 1995a, b).

New simulations realized by Haywood *et al.* (2002) with the HadAM3 AGCM coupled with the BIOME 4 vegetation model (Kaplan 2001) show that, due to higher temperatures and higher precipitation, Europe and the Mediterranean region were dominated by forest biomes during the Mid-Pliocene. This agrees with the pollen data, especially in higher latitudes where forests extended into what is now tundra. This confirms the good agreement between our pollen data and the HadAM3 AGCM.

Conclusion

A thorough review of existing pollen data has allowed us to present a regional climate synthesis for the Neogene, from the Middle Miocene (c. 14–15 Ma) to the Middle Pliocene (c. 3.5 Ma).

In Western Europe and the Mediterranean region, from the Middle Miocene to the Middle Pliocene, the vegetation cover reflects a clear latitudinal gradient. In all of the considered periods, the quantitatively reconstructed climate shows, in comparison to today, higher mean annual temperatures along the gradient and increases in mean annual precipitation in northwestern Europe and the northwestern Mediterranean, but similar precipitation to today in the southwestern Mediterranean region. The results also show a clear latitudinal gradient of temperature and precipitation, increasing for temperatures but decreasing for precipitation from north to south.

The results show that the thermic gradient has evolved in time. During the Middle Miocene, the presence of mega-mesothermic taxa in pollen spectra at all sites, even in Switzerland, shows that the thermic latitudinal gradient was weaker than the modern one. Based on the climate reconstructed from pollen data, the thermic gradient was around 0.48 °C per degree of latitude whereas it is today around 0.6 °C degree in Western Europe. This result is in agreement with estimations obtained from fossil floras of Europe (Bruch *et al.* 2004) and America (Liu & Leopold 1994). During the Tortonian and the Pliocene, the vegetation distribution and the climate reconstruction show the thermic latitudinal gradient to have been close to the modern one. The transition from the weak thermic latitudinal gradient of the Mid-Miocene to the modern-like gradient of the Pliocene appears

to take place during the Middle–Late Miocene, before or during the Tortonian.

The precipitation gradient was more accentuated than today from the Mid-Miocene to the Mid-Pliocene: the precipitation anomalies between the Neogene and today are larger in the north than in the south. The transition from this pattern to the modern latitudinal gradient took place after the Mid-Pliocene, at time of the first glacial–interglacial cycles.

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Quantifying the Eocene to Pleistocene topographic evolution of the southwestern Alps, France and Italy [☆]



Séverine Fauquette^{a,*}, Matthias Bernet^b, Jean-Pierre Suc^{c,d}, Anne-Sabine Grosjean^{e,f}, Stéphane Guillot^b, Peter van der Beek^b, Sébastien Jourdan^b, Speranta-Maria Popescu^g, Gonzalo Jiménez-Moreno^h, Adele Bertiniⁱ, Bernard Pittet^e, Pierre Tricart^b, Thierry Dumont^b, Stéphane Schwartz^b, Zhuo Zheng^j, Emile Roche^k, Giulio Pavia^l, Véronique Gardien^e

^a Institut des Sciences de l'Evolution, Université Montpellier 2, CNRS 5554, IRD, CC 061, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France

^b ISTerre, Université Grenoble Alpes, CNRS, 1381 Rue de la Piscine, 38041 Grenoble Cedex, France

^c Sorbonne Universités, UPMC Univ. Paris 06, UMR 7193, Institut des Sciences de la Terre Paris (iSTeP), F-75005 Paris, France

^d CNRS, UMR 7193, Institut des Sciences de la Terre Paris (iSTeP), F-75005 Paris, France

^e Laboratoire de Géologie de Lyon, Université Lyon 1/ENS Lyon, UMR 5276 CNRS, 2, Rue Raphaël Dubois, 69622 Villeurbanne Cedex, France

^f Laboratoire Magmas et Volcans, UMR CNRS 6524, Université Jean Monnet Saint-Etienne, 23 Rue Dr Paul Michelon, 42023 Saint-Etienne, France

^g GeoBioStratData.Consulting, 385 route du Mas Rillier, 69140 Rillieux la Pape, France

^h Departamento de Estratigrafía y Paleontología, Universidad de Granada, Fuente Nueva S/N, 18002 Granada, Spain

ⁱ Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira, 4, 50121 Firenze, Italy

^j Department of Earth Sciences, Sun Yat-sen University, Guangzhou 510275, China

^k Université de Liège, Unité de Paléobotanique, de Paléopalynologie et de Micropaléontologie, Sart Tilman, Allée du 6 Août, B.18, 4000 Liège 1, Belgium

^l Dipartimento di Scienze della Terra, Università di Torino, Via Valperga 35, 10125 Torino, Italy

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ABSTRACT

We evaluate the topographic evolution of the southwestern Alps using Eocene to Pleistocene pollen data combined with existing sedimentological, petrographic and detrital geo- and thermochronological data. We report 32 new pollen analyses from 10 sites completed by an existing dataset of 83 samples from 14 localities situated across the southwestern Alps, including both the pro- and the retro-foreland basins. The presence of microthermic tree pollen (mainly *Abies*, *Picea*) indicates that this part of the mountain belt attained elevations over 1900 m as early as the Oligocene. Inferred rapid surface uplift during the mid-Oligocene coincided with a previously documented brief phase of rapid erosional exhumation, when maximum erosion rates may have reached values of up to 1.5–2 km/Myr. Slower long-term average exhumation rates of ~0.3 km/Myr since the Late Oligocene helped maintaining the high Alpine topography of the southwestern Alps until today. The relative abundances of meso-microthermic tree pollen (*Cathaya*, *Cedrus* and *Tsuga*) and microthermic tree pollen (*Abies*, *Picea*) in the pro- and retro-foreland basin deposits, indicate that the present-day asymmetric topography, with a relatively gentle western flank and steeper eastern flank, was established early in the southwestern Alps, at least since

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* Corresponding author. Tel.: +33 4 67 14 41 79.

E-mail addresses: severine.fauquette@univ-montp2.fr (S. Fauquette), matthias.bernet@ujf-grenoble.fr (M. Bernet), jeanpierre.suc@gmail.com (J.-P. Suc), annesabine.grosjean@gmail.com (A.-S. Grosjean), s.guillot@ujf-grenoble.fr (S. Guillot), pvdbeek@ujf-grenoble.fr (P. van der Beek), sebastien.p.jourdan@gmail.com (S. Jourdan), speranta.popescu@gmail.com (S.-M. Popescu), gonzaloj@ugr.es (G. Jiménez-Moreno), adele.bertini@unifi.it (A. Bertini), bernard.pittet@univ-lyon1.fr (B. Pittet), Pierre.Tricart@ujf-grenoble.fr (P. Tricart), tdumont@ujf-grenoble.fr (T. Dumont), stephane.schwartz@ujf-grenoble.fr (S. Schwartz), eeszzhuo@mail.sysu.edu.cn (Z. Zheng), rocheemile@yahoo.fr (E. Roche), giulio.pavia@unito.it (G. Pavia), Veronique.Gardien@univ-lyon1.fr (V. Gardien).

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the Early Miocene, and possibly since the Oligocene or Late Eocene. Therefore, the high topography and asymmetric morphology of this part of the Alps has been maintained throughout the past ~30 Ma.

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1. Introduction

The topography of mountain belts reflects the combined effects and feedback relationships between tectonic processes, which cause crustal thickening and surface uplift, and climatically modulated surface processes, which create relief and tend to wear down mountainous topography (Willett, 1999; Whipple, 2009). Climate, in particular the amount, type and temporal distribution of precipitation, exerts a first-order control on weathering and erosion. The associated exhumation of rocks and mass redistribution at the surface influence the stress state and thermal structure of an orogen as part of the feedbacks within the system (Beaumont et al., 1992; Willett, 1999; Whipple and Meade, 2006). Different mechanisms have been proposed to explain the present-day topography and exhumation patterns of the European Alps, including crustal tectonics (Persaud and Pfiffner, 2004; Lardeaux et al., 2006), deep-seated geodynamic processes (Lyon-Caen and Molnar, 1989; Sinclair, 1997a; Lippitsch et al., 2003; Kuhlemann, 2007; Baran et al., 2014) or climatically induced processes. In particular the spatial coincidence of the highest rock-uplift rates in areas of the largest relief and the most deeply incised glacial valleys suggest that a significant part of the currently observed surface uplift is driven by the isostatic response to Quaternary glacial erosion of the mountain belt (Schlunegger and Hinderer, 2001; Champagnac et al., 2007; Vernon et al., 2009).

The tectonic record within the interior of the belt suggests a complex evolution with an exhumation signal that varies strongly both spatially and temporally (Garzanti and Malusà, 2008; Morag et al., 2008; Glotzbach et al., 2009; Jourdan et al., 2013). In particular, the exhumation history of the internal zones of the Alps, characterized by an Alpine metamorphic overprint, contrasts strongly with that of the external massifs (Vernon et al., 2008; Beucher et al., 2012). This evolution, however, appears smoothed in the regional detrital record, leading to an apparent constancy of exhumation rates recorded by detrital thermochronology data (Bernet et al., 2001, 2009; Glotzbach et al., 2011; Bernet, 2013).

Initial subaerial exposure and erosional exhumation of the internal zones of the Western Alps may have occurred during the climax of collision and major backthrusting of the internal zones at ~30 Ma (Fügenshuh and Schmid, 2003; Tricart et al., 2006) as well as overfilling of the peripheral foreland basins (Sinclair, 1997b; Ford et al., 1999; Pfiffner et al., 2002; Ford and Lickorish, 2004; Jourdan et al., 2012; Schwartz et al., 2012). A second major event took place during Early Miocene times, when extensional reactivation of the Oligocene frontal thrust (Penninic thrust) led to a shift in the locus of maximum surface uplift from the internal to the external zones of the Western Alps (Sue et al., 2007; Tricart et al., 2007). Surface uplift of the external crystalline massifs since this time (Leloup et al., 2005) led to drainage reorganization from a radial to the present longitudinal pattern and thus influenced sediment routing systems (Schlunegger et al., 1998; Kühni and Pfiffner, 2001).

We address two key questions: (1) What have been the magnitude and tempo of the elevation changes in the past? (2) Since when has the Alpine topography been comparable to the present-day?

Our reconstruction of the topography of the southwestern Alps since the onset of collision in the Late Eocene is based on the record of synorogenic pro- and retro-foreland basin (sensu Naylor and Sinclair, 2008) deposits of the southwestern part of the belt.

We use pollen analyses from Eocene and younger sediments coupled with previously published sedimentological, petrological, geochemical and geo-thermochronological sediment provenance and exhumation-rate data (Grosjean et al., 2012; Jourdan et al., 2012, 2013; Schwartz et al., 2012). We focus on two key phases, the Early Oligocene (~34–28 Ma), when collisional tectonics affected the entire mountain belt, and the Miocene (23.5–5.3 Ma), when major decoupling occurred between the external and internal zones along the Penninic front. The depositional age of the studied units is based on published biostratigraphic data and on climatostratigraphic correlation with other well-dated pollen floras from the northwestern Mediterranean (Suc et al., 1995a, 1999; Fauquette et al., 2007; Jiménez-Moreno and Suc, 2007; Bertini and Martinetto, 2008). Latest Messinian to Pleistocene pollen floras (Fauquette et al., 2006) have also been considered to provide insights on the topographic evolution through time.

2. Geological and morphological setting

2.1. Structure of the western Alps

The European Alps result from closure of the Alpine Tethys Ocean followed by continental collision between the European and Adriatic plates since ~35 Ma (Schmid et al., 2004; Rosenbaum and Lister, 2005). The structure of the belt is characterized by a complex nappe stack, involving both basement and cover rocks of the European margin, the intervening ocean (Piedmont zone) and micro-continents, and the Adriatic margin. The Penninic front, a crustal-scale thrust fault, separates the western Alps into an internal and an external domain (Fig. 1). The internal western Alps consist, from east to west, of (1) high-pressure/low-temperature metamorphic rocks of the internal crystalline massifs representing the most distal European margin (Dora-Maira, Gran Paradiso, Monte Rosa); (2) the Piedmont (“Schistes Lustrés”) zone; (3) medium to low-grade metamorphic rocks of the Briançonnais zone (European margin); (4) the non-metamorphic Helminthoid flysch nappes and (5) the obducted Chénaillet ophiolite (Fig. 1). The external western Alps, to the west of the Penninic front, include the External Crystalline Massifs (Mont Blanc, Aiguilles Rouges, Belledonne, Pelvoux, Argentera-Mercantour), which consist of European basement rocks that were metamorphosed and intruded by granites during the Variscan orogeny, as well as Permo-Triassic to Cretaceous sedimentary cover rocks of the former European passive margin (Fig. 1).

2.2. Present-day topography

The present-day mean elevation of the western Alps is ~1500 m, with about 60 mountain peaks over 4000 m in the Mont Blanc, Valais, Monte Rosa and Pelvoux massifs (Fig. 2A). Local relief reaches between 2000–3000 m in the northwestern and 1000–2000 m in the southwestern Alps (Vernon et al., 2009). Although the highest summits and relief are associated with the External Crystalline Massifs, the internal zones have the highest average topography. Topographic profiles across the north-, central- and south-western Alps (Fig. 2B) show a clear asymmetric topography, with a steep eastern flank and a somewhat gentler western flank.

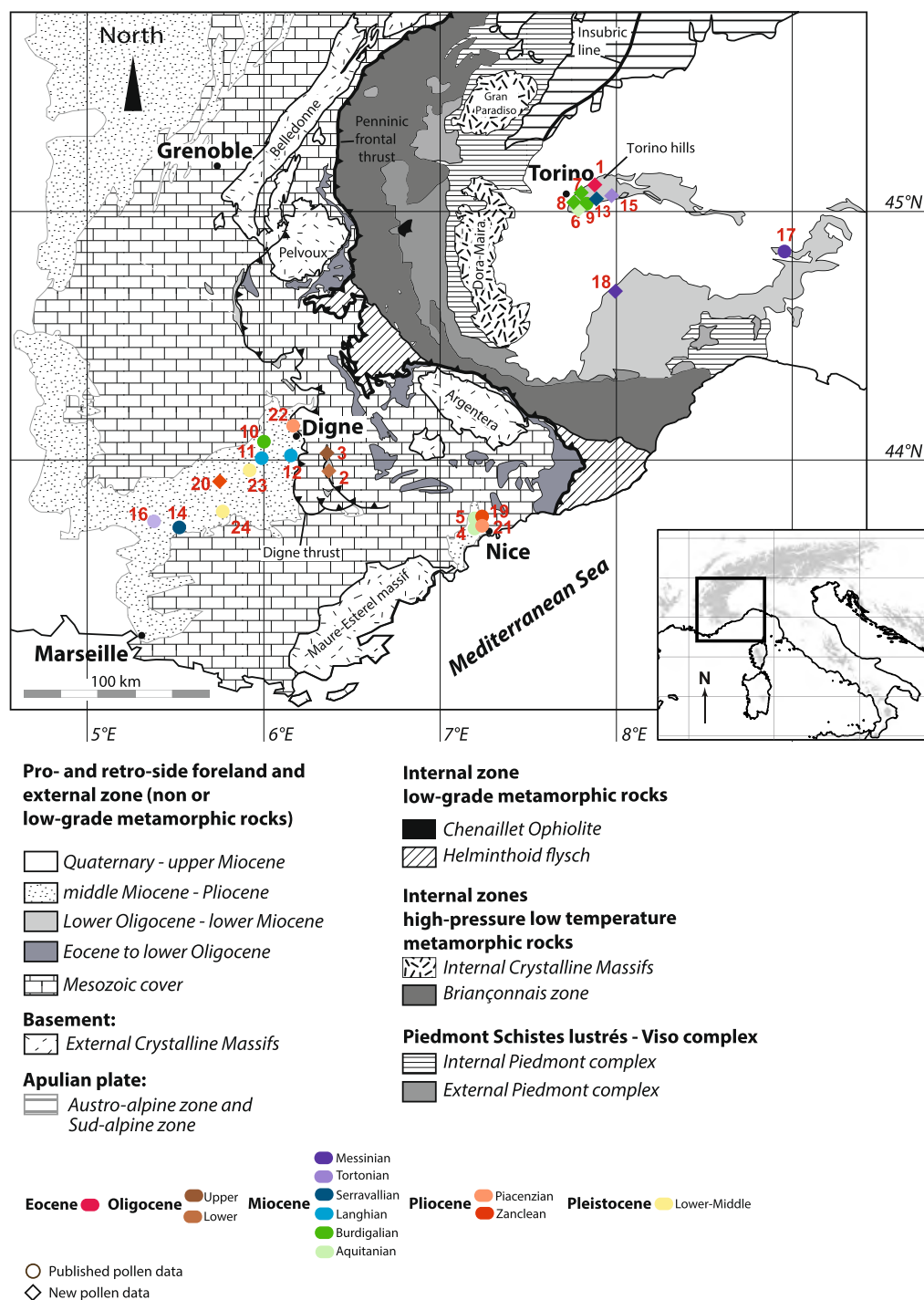


Fig. 1. Simplified geological map of the western Alps (modified from Jourdan et al., 2012) showing the location of the Paleogene to Neogene pollen sites. Pollen sites are numbered according to stratigraphic age: 1, Gassino Torinese; 2, Saint-Lions; 3, Gambi; 4, Le Gour; 5, Carros; 6, Tetti Civera 1; 7, Tetti Civera 2; 8, Tetti Civera 3; 9, Rio Civera; 10, La Rosée; 11, Les Mées 1 (borehole); 12, Châteauredon; 13, Pavarolo; 14, La Motte d'Aigues; 15, Borelli; 16, Vaugines; 17, Torre Sterpi; 18, Sioneri; 19, Saint-Martin du Var; 20, Villeneuve; 21, Saint-Isidore; 22, Le Rochassas; 23, Les Mées-Périgoite; 24, Orasion-Flour. New pollen data are indicated by a diamond and published pollen data by a circle.

3. Data and methods

3.1. Modern pollen records

Two transects were sampled across the southwestern Alps (Fig. 3 and Supplementary Table 1A) to obtain the pollen image of present-day vegetation. The pollen data (20 moss polsters and 2 recent lake sediments) are compared to the vegetation distribution along altitudinal and longitudinal gradients and are used as a

reference to interpret Paleogene to Quaternary pollen records. The moss polsters have been processed using KOH (10%), whereas lake sediments were treated with HCl and HF, both before sieving at 10 µm. Up to ~150 pollen grains were counted, excluding *Pinus* generally over-represented in pollen data.

3.2. Late Eocene to Mid-Pleistocene pollen records

We searched for pollen grains in clayey sediments (see Tables 1 and 2 for information on their deposition environment)

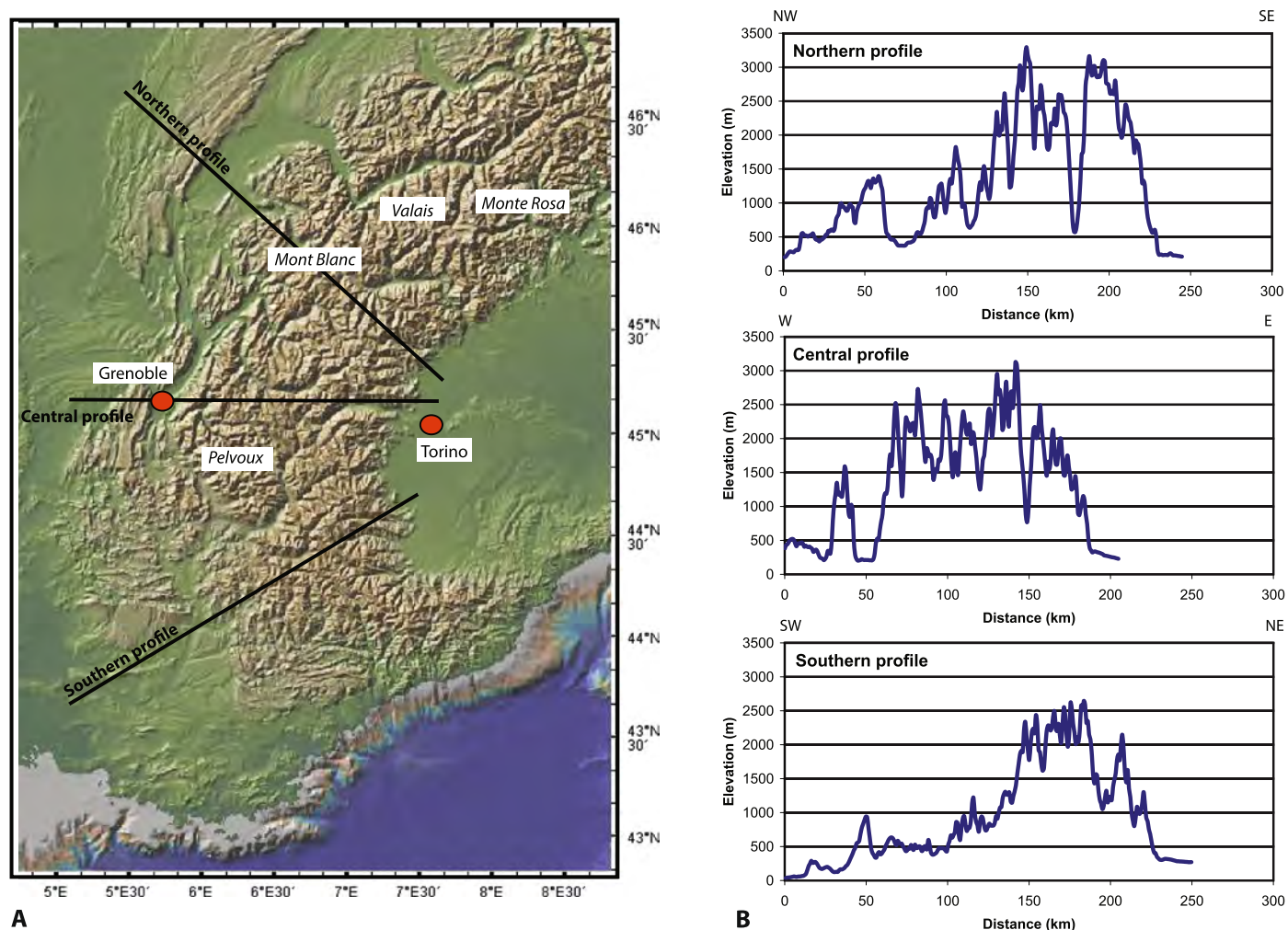


Fig. 2. A) Topographic map of the western Alps with the location of the areas with mountain peaks over >4000 m elevation (Mont Blanc, Valais, Monte Rosa, and Pelvoux) and B) three east–west profiles in the northern, central and southern parts of the western Alps. Particularly the northern and southern profiles show the asymmetric topography of the Western Alps with a steep eastern flank and a gentler western flank. The map was made with the GeoMap App (<http://www.geomapapp.org>), using the Global Multi-Resolution Topography (GMRT) basemap (Ryan et al., 2009).

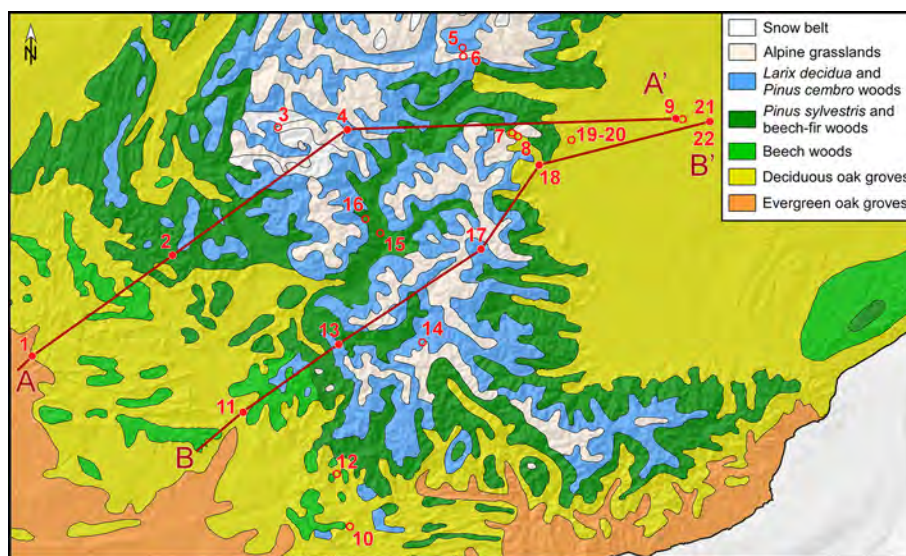


Fig. 3. Simplified vegetation map of the southwestern Alps (from Noirfalise et al., 1987) and position of the two transects along which modern pollen data were collected (localities on the transects are indicated by dots, localities out of the transects by circles). The relief of the map was added using the GeoMap App (<http://www.geomapapp.org>) (Ryan et al., 2009). See Supplementary Table 1 for details on the localities.

Table 1

Results of the palaeo-elevation estimates for marine sediment sites. For each site we report the age and depositional environment of the sediments, the palaeolatitude based on the palaeogeographic maps of [Meulenkamp and Sissingh \(2003\)](#), the estimated mean annual temperature from pollen data (minimum, Most Likely Value, maximum MAT), the shift in altitude of the vegetation belts due to the differences in temperature with respect to the present-day, the most probable palaeo-elevations of the nearby massifs based on the Most Likely Values of MAT and, in brackets, ranges of palaeo-elevations based on the minimum and maximum MAT.

	Sites	Age	Depositional environment	Palaeo-latitude (°N)	MAT (°C) Min – MLV – max	Shift in altitude (m)	Microthermic trees in pollen records	Palaeoaltitude of nearby massifs
French slope	21 Saint-Isidore	Early Piacenzan	Marine, deltaic	Modern	14.8 – 17 – 18.2	+265 + 640 + 860	<i>Abies</i> , <i>Picea</i> , <i>Cathaya</i> , <i>Cedrus</i>	2040 m (1665/2260)
	20 Villeneuve Pigeonnier de l'Ange	Middle Zanclean	Marine, deltaic	Modern	11.9 – 16.5 – 24.7		<i>Cathaya</i>	950 to 1800 m
	19 Saint-Martin du Var	Latest Messinian to Early Zanclean	Marine, deltaic	Modern	15 – 16.5 – 18.6	+300 + 541 + 930	<i>Abies</i> , <i>Picea</i> , <i>Cathaya</i> , <i>Cedrus</i>	1940 m (1700/2330)
	16 Vaugines	Late Tortonian	Palustrine	41	10 – 16.8 – 22.8	–1000 + 270 + 1460	<i>Abies</i> , <i>Picea</i> , <i>Cathaya</i>	1670 m (400/2860)
	14 La Motte d'Aigues	Latest Serravallian	Marine, embayment	38	16 – 17.9 – 22.8		Very rare <i>Cathaya</i>	Low altitude
	12 Châteauredon	Early Langhian	Marine, embayment	38.2	17.4 – 19.7 – 22.8		Very rare <i>Cathaya</i>	Low altitude
	11 Les Mées (borehole)	Latest Burdigalian to early Serravallian	Marine, embayment	38	17 – 18.8 – 21.8		<i>Cathaya</i> , very rare <i>Abies</i> , <i>Picea</i> , <i>Cedrus</i>	Low altitude
	10 La Rosée	Late Burdigalian	Marine, embayment		15 – 20 – 24.5		Less than 1% of <i>Picea</i> , no <i>Abies</i> , few <i>Cathaya</i>	950 to 1800 m
	4 Le Gourg	Latest Aquitanian	Marine, embayment	37.2	16.8 – 19.4 – 24.7		Less than 1% of <i>Picea</i> and <i>Abies</i> , few <i>Cathaya</i> and <i>Cedrus</i>	950 to 1800 m
	5 Carros	Aquitania	Marine, embayment	37.2	16.8 – 19.4 – 24.7		<i>Cathaya</i> , <i>Cedrus</i> , very rare <i>Picea</i> and <i>Abies</i>	950 to 1800 m
	3 Gambi	Chattian	Marine, deltaic	38	15.6 – 18.8 – 24.7	–290 + 340 + 1500	<i>Cathaya</i> , <i>Picea</i> , <i>Cedrus</i> , very rare <i>Abies</i>	1740 m (1110/2900)
	2 Saint-Lions	Rupelian	Marine, deltaic	38	15.6 – 19.6 – 24.7	–290 + 500 + 1500	<i>Cathaya</i> , <i>Cedrus</i> , <i>Picea</i>	1900 m (1110/2900)
	17 Torre Sterpi	Latest Messinian	Lagoonal	41.5	15.6 – 17.6 – 20	+90 + 485 + 960	Mostly <i>Cathaya</i> , <i>Cedrus</i> , <i>Picea</i> , <i>Abies</i>	1785 m (1400/2260)
Italian slope	18 Sioneri	Latest Messinian	Lagoonal	41.5	15.6 – 17.7 – 22.8	+90 + 500 + 960	Mostly <i>Picea</i> , <i>Abies</i> , <i>Cedrus</i> , <i>Cathaya</i>	1800 m (1390/2800)
	15 Borelli	Middle Tortonian	Marine, embayment	42.4	15.5 – 17.8 – 22.8	+165 + 625 + 1600	<i>Abies</i> , <i>Picea</i> , <i>Cathaya</i> , <i>Cedrus</i>	1925 m (1465/2900)
	13 Pavarolo	Serravallian	Marine, embayment	40	17 – 19 – 24.7	+200 + 600 + 1700	<i>Abies</i> , <i>Picea</i> , <i>Cathaya</i> , <i>Cedrus</i>	1900 m (1500/3000)
	9 Rio Civera	Late Burdigalian	Marine, embayment	39.5	15.7 – 18.7 – 21.7	–110 + 480 + 1080	Very rare <i>Abies</i> and <i>Cedrus</i> , mostly <i>Cathaya</i>	1780 m (1200/2380)
	8 Tetti Civera 3	Middle Burdigalian	Marine, embayment	39.5	15.6 – 19 – 24.7	–130 + 540 + 1650	<i>Abies</i> , <i>Picea</i> , <i>Cathaya</i> , <i>Cedrus</i>	1840 m (1170/2950)
	7 Tetti Civera 2	Early Burdigalian	Marine, embayment	39.5	15.6 – 18.8 – 24.7	–130 + 500 + 1650		1800 m (1170/2950)
	6 Tetti Civera 1	Aquitania	Marine, embayment	38.5	16.8 – 18.7 – 21.6	+0 + 380 + 950		1680 m (1300/2250)
	1 Gassino Torinese	Priabonian	Marine, embayment	36	15 – 19.2 – 24.7		<i>Cathaya</i> , very rare <i>Picea</i>	950 to 1800 m

Table 2

Results of the palaeo-elevation estimates for non-marine sediment sites. For each site we report the modern elevation, the age and depositional environment of the sediments, the Most Likely Value of MAT, the contemporaneous flora living in lowlands used for the comparison and the palaeo-elevation of the site.

Non-marine sediment sites	Modern elevation (m)	Age	Depositional environment	MLV of MAT (°C)	Contemporaneous flora living in lowlands	Paleoaltitude of the sites
24 Oraison – Flour	408	Early Pleistocene	Fluvial loams	14.8	Semaforo (Southern Italy, Fauquette and Combourieu-Nebout, 2013)	420 m
23 Les Mées – Périgoite	522	Early Pleistocene	Fluvial loams	15.2	St Isidore (Southern France, Zheng and Cravatte, 1986)	330 m
22 Le Rochassas	820	Piacenzian	Palustrine	12	Mirabel (Naud and Suc, 1975)	890 m
16 Vaugines	430	Tortonian	Palustrine	16.8		~0

sampled close to coarser deposits in which mineralogical and thermochronological studies were performed previously. Most samples were collected from marine deposits of the foreland basins of the developing Alps, where abundant detrital sediments were supplied by the developing orogenic drainage system. In such sediments, pollen floras provide an unbiased record of the regional vegetation altitudinal belts, as established by studies on recent sediments (Heusser and Balsam, 1977; Heusser, 1988; Cambon et al., 1997; Beaudouin et al., 2005, 2007). A few samples have been collected in continental lacustrine, fluvial or lagoonal deposits.

Thirty-two new samples from 10 localities complete an existing dataset of 83 samples from 14 localities (Bessedik, 1985; Zheng and Cravatte, 1986; Zheng, 1990; Jiménez-Moreno, 2005; Suc et al., 1999; Hippolyte et al., 2011; Dubar, 1979). The total dataset thus contains data from 24 localities ranging from Late Eocene to Lower-Middle Pleistocene and distributed spatially on both flanks of the southwestern Alps (Fig. 1 and Supplementary Table 1B). Pollen identification following the botanical classification, based on high-level morphological examination, was accomplished at the finest possible taxonomic level by comparing the Paleogene and Neogene pollen grains with their present-day relatives using modern pollen collections. Percentages of taxa were calculated on the sum of the pollen grains and standard synthetic diagrams were drawn (Suc, 1984).

3.3. Methods for estimating palaeo-elevations using pollen data

The methods to quantify palaeo-elevations, developed by Fauquette et al. (1999) and Suc and Fauquette (2012) take into account pollen floras that provide a regional view of the vegetation from the lowermost up to the uppermost altitudinal belts within the drainage basin from which the sediments were sourced. The vertical shift of vegetation belts with latitude is obvious but difficult to quantify, as the altitudinal range of plant species is controlled by climatic parameters (decreasing temperature with altitude/latitude and concomitant increasing precipitation), but also by local conditions such as the nature of soils, slope orientation, etc. This organization of the vegetation was used by Ozenda (1975, 1989, 2002) to establish a standard relationship in which modern vegetation belts shift 110 m in altitude per degree in latitude ($0.6^\circ\text{C}/^\circ$ latitude vs. $0.55^\circ\text{C}/100$ m elevation). This relationship seems to be valid for all mountainous massifs of the northern hemisphere, between 70° and 30°N (Ozenda, 1989). The validity of the relationship is also demonstrated by detailed studies of the altitudinal limits of the vegetation in the Atlas Mountains of Morocco (Ozenda, 1975) and in the central Himalaya (Dobremez, 1972). The effect of the continentality may be important but our Neogene sites are situated in similar longitudinal position as the Alps today, so temporal variations in continentality will have been minimal. Therefore, using this altitude–latitude relationship together with the vegetation distribution and climatic estimates, palaeo-elevations may be assessed using fossil pollen records.

Microthermic trees inhabiting high elevation/high latitude zones, such as *Abies* and *Picea*, represent the best indicators of elevated topography in the fossil pollen floras. Based on modern marine sediments close to the Alps (Suc et al., 1999), a threshold value of $\sim 3\%$ for *Abies* and *Picea* has been used to infer the presence of forests of these taxa in the past (Fauquette et al., 1999). Nevertheless, pollen data do not allow estimating the altitudinal range of this vegetation belt, nor whether Alpine herbaceous and perpetual-snow belts existed above. This limitation is due to the difficulty of differentiating alpine herbaceous elements from those growing at lower elevations. As a consequence, these pollen-based palaeo-elevations are minimum estimates corresponding to the lower limit of the highest forested belt.

Palaeo-elevation estimates are based on the mean annual temperature (MAT) estimated at low elevations by excluding microthermic taxa from the reconstruction process (Fauquette et al., 1998). This low-elevation temperature is subsequently used as the base to estimate minimum elevation in the source area of the sediments using the full pollen spectrum and the relation between altitudinal and latitudinal temperature gradients inferred by Ozenda (1975, 1989, 2002). This procedure allows us to discriminate climatic variations from elevation changes.

Before the Tortonian, the latitudinal temperature gradient was weaker than the modern one in Europe; it was estimated by Fauquette et al. (2007) to be around $0.48^\circ\text{C}/^\circ$ latitude during the Middle Miocene. We have similarly reconstructed the latitudinal temperature gradient for the Early Oligocene (Rupelian, 34–28 Ma) based on the MAT assessed from pollen records from significantly different palaeo-latitudes: Tongres, Belgium ($50^\circ 46'\text{N}$, Roche and Schuler, 1976) where $\text{MAT} = 17.5^\circ\text{C}$ and Montauban, southern France ($44^\circ 01'\text{N}$) where $\text{MAT} = 19.6^\circ\text{C}$ (Fig. 4 and Supplementary Table 2). We find that the Rupelian latitudinal temperature gradient was also weaker than the modern; around $0.46^\circ\text{C}/^\circ$ latitude. Hypothesizing that the ratio between altitudinal and latitudinal temperature gradients was similar to the present ratio during these times results in Rupelian and Middle-Miocene altitudinal temperature gradients of ca. 0.42°C and $0.44^\circ\text{C}/100$ m, respectively.

Prior to the Pliocene, Europe was situated at lower latitudes than today (Fig. 4; Meulenkamp and Sissingh, 2003). The palaeo-latitudes of the sites for which we have pollen data have therefore been estimated from palaeogeographic maps.

Our method for estimating palaeo-elevation from pollen data has previously been successfully applied to Early Pliocene (5.3 Ma) marine sediments from the foot of the Mercantour Massif, south-eastern France, where it was validated by quantitative geomorphology (Fauquette et al., 1999). More recently, similar analyses have been applied to the Eastern Alps (Jiménez-Moreno et al., 2008), the Eastern Pyrenees (Suc and Fauquette, 2012) and the Apennines (Fauquette and Combourieu-Nebout, 2013; Fauquette et al., in press).

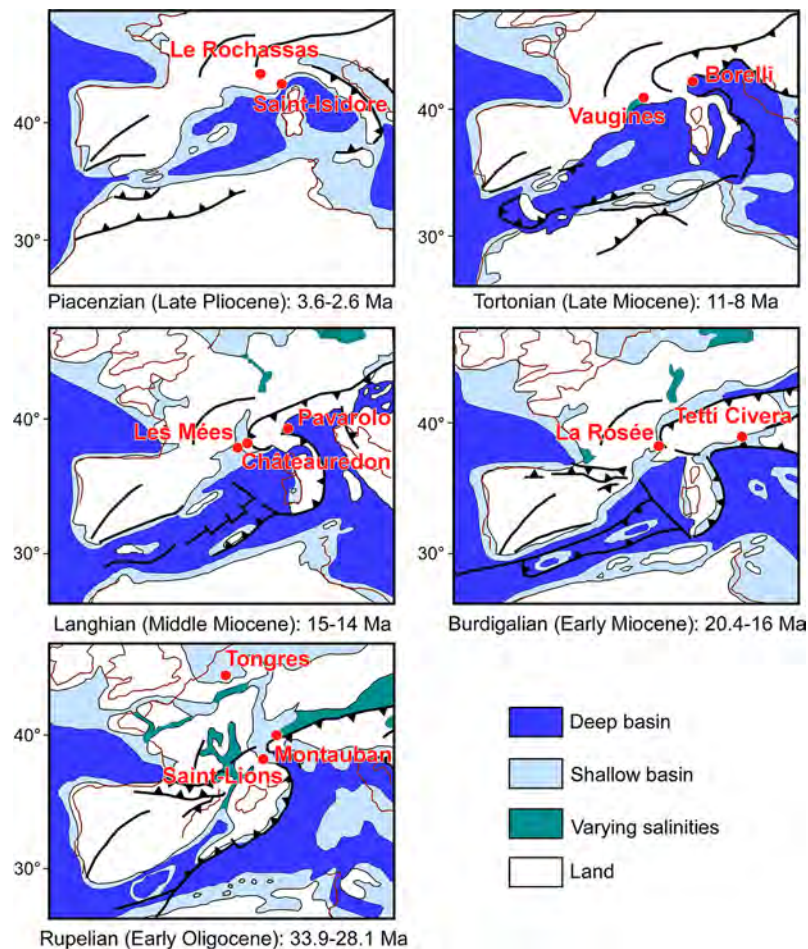


Fig. 4. Palaeogeographic maps (from Meulenkamp and Sissingh, 2003) with the position of the concerned sites for the late Rupelian, Burdigalian, Langhian, Tortonian and Piacenzian.

4. Results

4.1. Modern pollen flora transects

Vegetation is similarly organized in altitudinal belts on both flanks of the mountain belt except for the occurrence of the Mediterranean evergreen belt at low elevations to the west (Fig. 5). Vegetation belts are organized altitudinally according to the concomitant decrease in temperature and increase in precipitation, and are defined by their dominant plant element(s) (Noirfalise et al., 1987; Ozenda, 2002).

Pollen grains have been grouped as much as possible to correspond to vegetation belts (Fig. 5). However, several complications could not be avoided and require some explanation. First, *Pinus* has been separated because its pollen grain is not identifiable at the species level. Therefore, this genus may represent several vegetation belts, although its abundance in samples from the 'Larix decidua' and 'Pinus cembro woods' belt or close to it (sites 4, 5, 6, 13, 15; Fig. 5) allows considering a probable origin from this belt in such cases. Second, pollen grains of *Larix* are scarcely recorded; samples containing this genus were collected almost exclusively within its forests (sites 4, 5, 13, 15) or from sites immediately below such forests (sites 7, 8, 10, 12, 14, 16, 18). Third, pollen grains of Cupressaceae (rare except in site 22) are grouped because they cannot be identified at the genus level, even though their species grow at different altitudes (*Cupressus sempervirens* and *Juniperus oxycedrus* in the two lowermost vegetation belts, *J. communis* in the subalpine belt, *J. thurifera* at higher elevations). Fourth, most of the herbaceous pollen grains cannot be distinguished at an infra-

family level, whereas such plants can inhabit different altitudes; their abundance may indicate open (site 1) and/or undergrowth (sites 2, 3, 5, 7, 9, 14, 15, 18, 19, 20, 21) vegetation. Finally, alpine tundra-like plants (*Polygonum alpinum*, *Gentiana*, *Centaurea uniflora*) have been identified in some sites (4, 6, 13, 15), sometimes in large quantities. There, some other plants have been ascribed to this group by deduction such as *Alnus* ascribed to *A. viridis* and *Salix* to a dwarf willow despite our inability to identify them at the species level.

Wind transport may be important in mountainous regions and may lead to deposits recording pollen originating from other vegetation belts than that of the source area.

Despite these potential complications, the pollen data show a good correlation with the vegetation distribution along the slopes of the massifs and therefore faithfully record the different vegetation belts (Fig. 5). They also reflect the asymmetric elevation and therefore vegetation distribution along the two transects from west to east: the replacement of pollen groups as elevation increases appears progressive on the western flank but much more abrupt to the east (Fig. 5).

4.2. Late Eocene to Mid-Pleistocene pollen floras

Late Eocene to Pliocene pollen floras from both flanks of the southwestern Alps are characterized by prevalent megamesothermic plants (supporting subtropical conditions: MAT between 20 and 24 °C; Nix, 1982) and sometimes high frequencies of *Cathaya* (Fig. 6), a conifer living today in subtropical China at mid to high elevations, below the *Abies* and *Picea* belt (Wang,

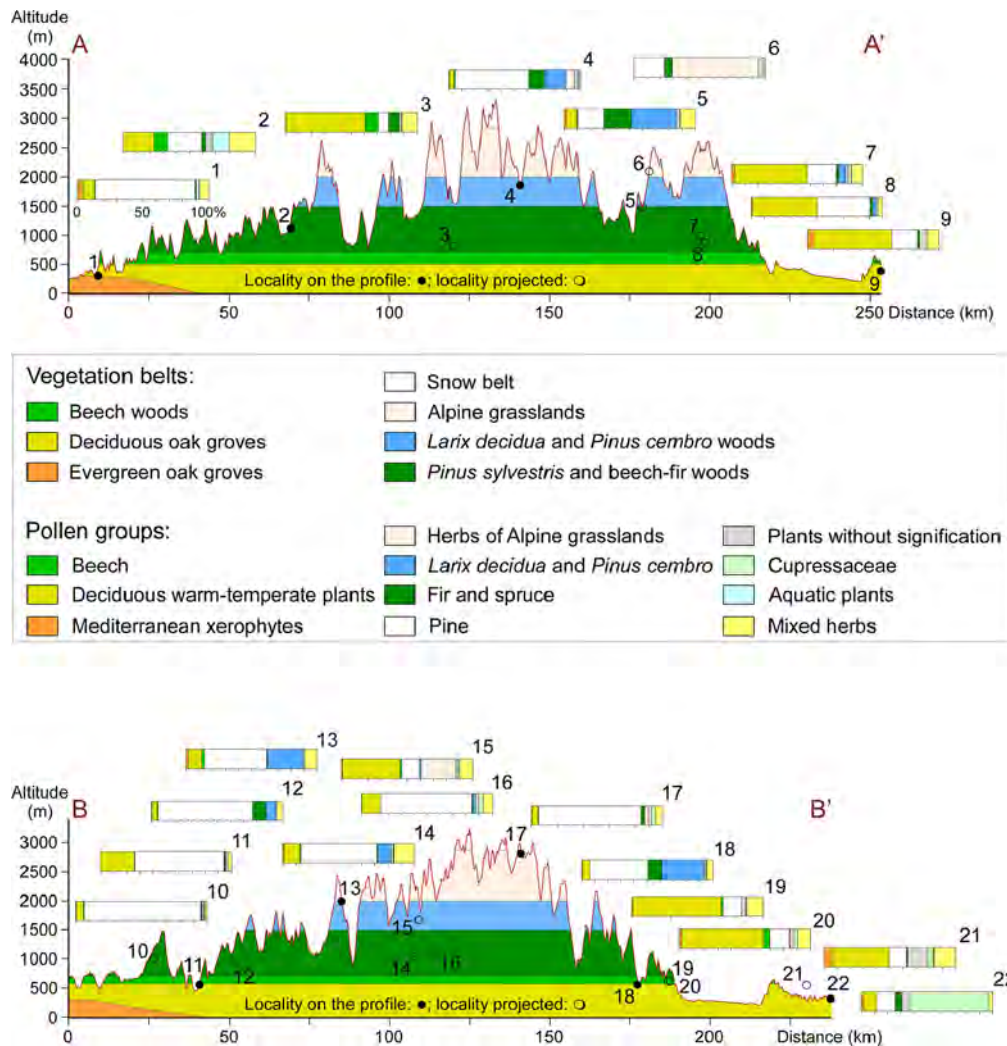


Fig. 5. Topography along the two transects of Fig. 3, position of the different vegetation belts (from Noirfalise et al., 1987; Ozenda, 2002) and relative proportions of pollen groups in the modern samples. Pollen localities are: Transect AA': 1, Nyons; 2, Luz la Croix haute; 3, Le Freney; 4, Col du Lautaret; 5–6, Mont Ceniz; 7, Pinerolese (Lago Villaretto di Roure); 8, Pinerolese (Balma di Roure); 9, Baldissero Torinese (Val Samfrà). Transect BB': 10, Taulanne; 11, Clumanc; 12, Sisteron; 13, Saint-Léger; 14, Lac de Séguret; 15, Fournel; 16, Roche de Rame; 17, Agnel; 18, Inverso Pinasca; 19–20, Cappella della Colletta di Cumiana; 21, Baldissero Torinese; 22, Moncucco Torinese.

1961). Megathermic plants (supporting tropical conditions: MAT $>24^{\circ}\text{C}$; Nix, 1982) are present in all Eocene to Middle Miocene samples. The maximum frequency of such species was observed at Châteauredon the early Langhian age of which (Besson et al., 2005; Jiménez-Moreno and Suc, 2007) corresponds to the Mid-Miocene Climatic Optimum (~ 15 Ma; Zachos et al., 2001, 2008). Megamesothermic pollen grains decrease from the early Zanclean (~ 5 Ma) to the Piacenzian (3.6–2.6 Ma) (Fig. 6) and disappear from the pollen records at the earliest Pleistocene (2.6 Ma), probably due to the onset of Northern Hemisphere glaciations (Suc and Zagwijn, 1983; Suc, 1984; Bertini, 2010; Popescu et al., 2010).

On the whole, microthermic trees (supporting boreal conditions: MAT $<12^{\circ}\text{C}$; Nix, 1982) such as *Abies* and *Picea* occur in significantly higher frequencies on the eastern flank (Tetti Civera, Pavarolo, Borelli) than in the west, except at Vaugines (late Tortonian), located at the foot of the Luberon Massif, where high percentages of *Abies* and *Cathaya* are recorded. From the Early Miocene to the beginning of the Tortonian, samples from the eastern flank also show a significant abundance of the meso-microthermic (supporting cool-temperate conditions: MAT between 12 and 14°C ; Nix, 1982) tree *Cedrus*, whereas at the same time *Cathaya* is the most frequent high-elevation tree recorded on the western flank (Fig. 6).

4.3. Palaeo-elevation estimates

The minimum estimated palaeo-elevation (corresponding to the lower limit of the *Abies-Picea* belt) is relatively well constrained for periods prior to the Pliocene, when climate was tropical to subtropical in Europe, because the uppermost vegetation belt was most likely forested rather than herbaceous. For the Plio-Pleistocene, the presence of alpine tundra-like vegetation is expected above the fir-spruce-larch forest. However, pollen data do not allow establishing the presence of an alpine herbaceous belt above the highest forest belt due to the difficulty of unambiguously discriminating high-altitude herbs from other herbaceous pollen. Palaeo-elevation estimates are thus minimum values, restricted to the lower limit of the highest forest belt. The results presented in Table 1 correspond to the most probable palaeo-elevations based on the Most Likely Values of MAT and, in brackets, to ranges of palaeo-elevations based on the minimum and maximum MAT.

Most of the sites to the east of the range (Tetti Civera, Rio Civera, Pavarolo, Borelli, Torre Sterpi, Sioneri; Fig. 1) record pollen grains of *Cathaya*, *Abies* and *Picea* (Fig. 6) indicating high palaeo-elevations within the nearby massifs. In Gassin Torinese (Late Eocene; Fig. 6) *Cathaya* is the only meso-microthermic tree present (Table 1), indicating an altitude between 950 and 1800 m. However, this is also the only site in our dataset that predates the

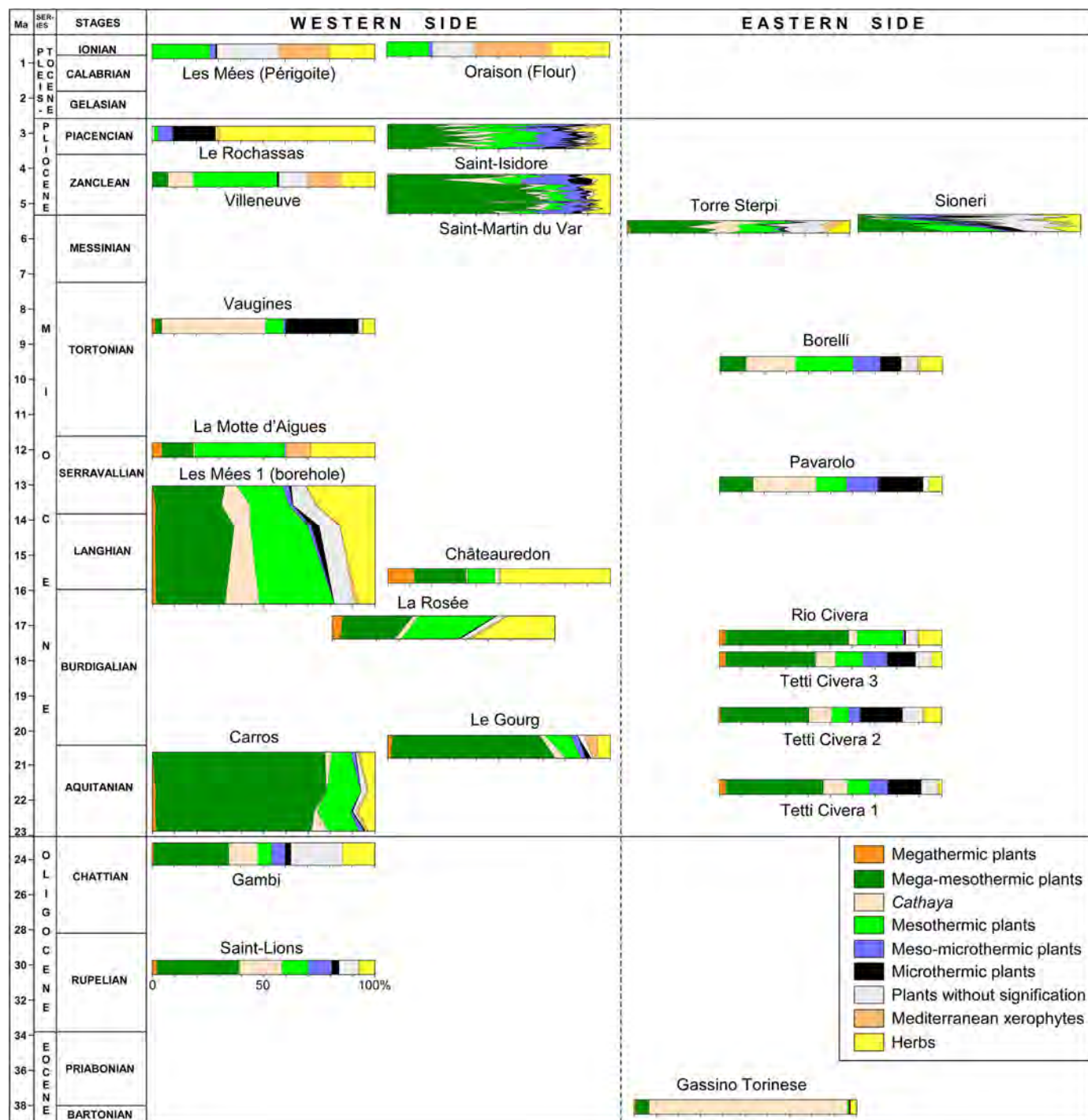


Fig. 6. Synthetic pollen diagrams for the Late Eocene to Pleistocene samples and their position in a chronostratigraphic frame (note the change of timescale at the Paleogene/Neogene boundary). Taxa have been arranged into thirteen different groups based on ecological criteria in order to visualize the main changes in the palaeo-vegetation cover at different altitudinal belts. Some groups are constituted according to thermic requirements of taxa with respect to the Nix (1982) classification based on the mean annual temperature (MAT): megathermic (tropical): $\text{MAT} > 24^\circ\text{C}$; mega-mesothermic (subtropical): $20^\circ\text{C} < \text{MAT} < 24^\circ\text{C}$; mesothermic (warm-temperate): $14^\circ\text{C} < \text{MAT} < 20^\circ\text{C}$; meso-microthermic (cool-temperate): $12^\circ\text{C} < \text{MAT} < 14^\circ\text{C}$; microthermic (boreal): $\text{MAT} < 12^\circ\text{C}$.

rapid Eocene–Oligocene cooling (Zachos et al., 2001; Hren et al., 2013). To the west of the southwestern Alps, the Oligocene Saint-Lions and Gambi sites (Figs. 1 and 6) indicate relatively high palaeo-elevations (1900 and 1740 m, respectively; Table 1). However, the other pre-Zanclan sites do not show significant percentages of *Abies* and *Picea*. In some sites (Châteauredon, La Motte d'Aigues; Table 1; Fig. 6) *Abies*, *Picea* and *Cathaya* are completely absent. Considering the La Motte d'Aigues site, this absence may be due to the long distance from high-elevation pollen sources. Data

from Châteauredon indicate the absence of high topography near this site. Early Zanclan to Early Piacenzian pollen data indicate high palaeo-elevations in the source areas, except at Villeneuve for which high-elevation trees are represented mostly by *Cathaya* (*Picea* < 1%; Table 1).

Table 2 displays the palaeo-elevation estimates for the continental sites. In this case, the estimated MLV of MAT from the pollen assemblage is compared to values inferred from a contemporaneous pollen flora representative of lowland vegetation.

The estimates correspond in this case to the palaeo-elevations of the pollen localities themselves. The analysis shows that the Late Pliocene–Pleistocene sediments of Oraison-Flour, Les Mées-Périgoite, Le Rochassas sites were deposited at their modern elevations of 408, 522 and 820 m respectively (Table 2). In contrast, the pollen assemblage from Vaugines (Tortonian), at the foot of the Luberon Massif (1125 m), indicates a very low elevation during deposition (Table 2); this site has therefore been uplifted later to attain its modern elevation of 430 m. However, the abundance of *Abies* and *Cathaya* in this pollen assemblage indicates nearby high elevations, estimated to be above 1670 m (Table 1).

5. Discussion

5.1. Limitations of the method

Numerous pollen studies (Roche and Schuler, 1976; Bessedik, 1985; Suc, 1989; Zheng, 1990; Suc et al., 1995a, 1995b, 1999; Jiménez-Moreno, 2005; Bertini and Martinetto, 2011) have shown that the European vegetation of the Mid-Cenozoic follows a similar latitudinal and altitudinal belting to that observed in present-day southeastern China (Wang, 1961) where most of the taxa that disappeared from Europe by the Late Neogene still occur today. One of the plants indicating the existence of significant palaeo-elevations in our pollen data is *Cathaya*. However, the use of this genus in palaeoenvironmental reconstructions is not straightforward as it is currently considered as a relictual plant. Modern *Cathaya* is a monospecific genus (*C. argyrophylla* Chun and Kuang) restricted to southern China (Wang, 1961). Eight populations have been recorded in four provinces (Guangxi, Hunan, Sichuan, Guizhou; Mao, 1989). They are found between 950 and 1840 m elevation at latitudes between around 24° and 29°N. Thus, the modern habitat of *Cathaya* is located ~10° more to the south than the palaeo-latitudes of the Cenozoic western Alps sites (Fig. 4). However, present-day isotherms are also shifted ~10° in latitude to the south in eastern China in comparison to Europe. For our reconstructions, we thus consider minimum and maximum elevations of 950 m and 1800 m, respectively, for *Cathaya*.

The altitude estimates of the sites were calculated using the Most Likely Values (MLV) of mean annual temperature (MAT) obtained from the pollen data. Although MLVs are less informative of climate than the entire reconstructed climatic amplitudes, as plants may sometimes support large climatic ranges, they provide a good estimation of the optimum conditions where the encountered plant assemblages best develop. Moreover, MLVs have been statistically tested on modern pollen data and are considered to provide reliable results (Fauquette et al., 1998). However, in order to provide an idea of the uncertainties, we also report the palaeo-elevation estimates based on the minimum and maximum MAT (in brackets in Table 1).

We combine our pollen data with multiproxy provenance analyses from the same detrital sediments (Jourdan et al., 2012), together with reconstructions of the drainage network (Grosjean et al., 2012) in order to better constrain pollen sources. We can use this data because studies on recent marine coastal sediments have established that the contribution of airborne pollen to these sediments is negligible in comparison to fluvially transported pollen (Cambon et al., 1997; Beaudouin et al., 2007).

5.2. Evolution of the western flank

Rupelian sediments sampled in the Barrême Basin at Saint-Lions (Fig. 1) were sourced from the internal Alpine massifs (Piedmont zone close to the modern Monte Viso and Briançonnais zones), whereas Chattian sediments from the nearby Gambi site are dominated by local clastic input mixed with a low proportion

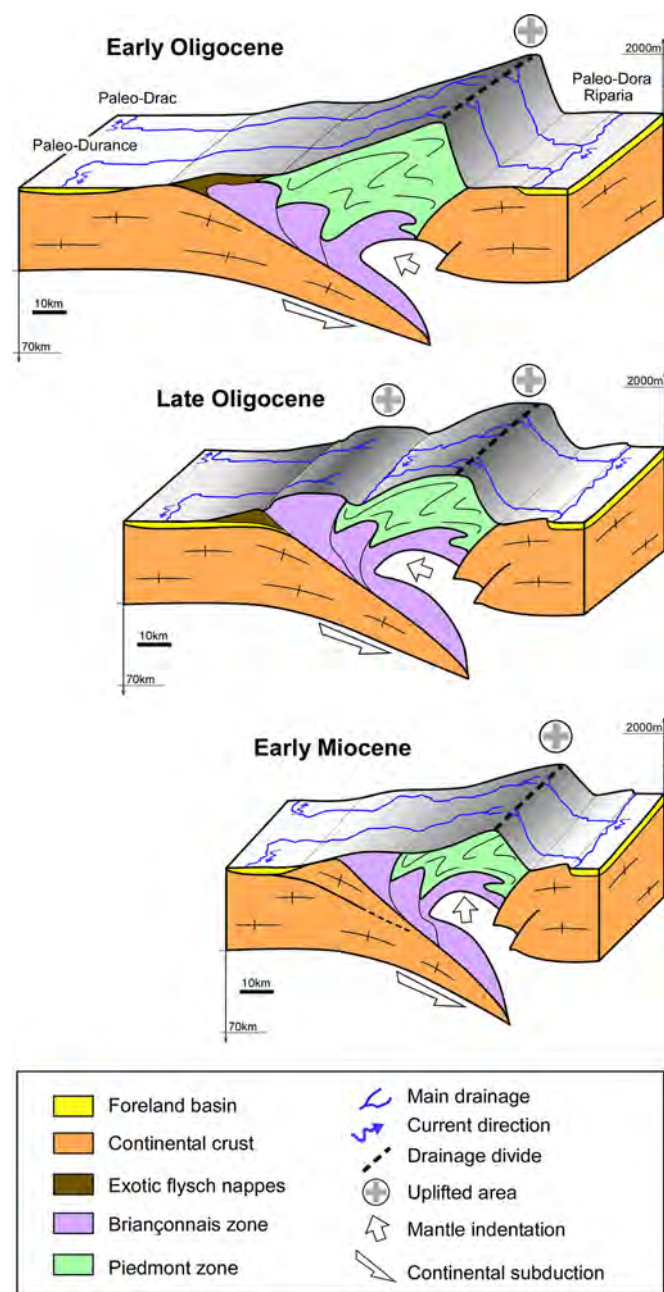


Fig. 7. Schematic reconstruction of the topographic and drainage evolution of the southwestern Alps from Early Oligocene to Early Miocene, showing the palaeo-Durance and the palaeo-Drac rivers draining the western flank of the main divide and the palaeo-Dora-Riparia draining the eastern flank.

of Alpine detritus (Evans and Mange-Rajetzky, 1991; Evans and Elliott, 1999; Morag et al., 2008; Jourdan et al., 2012; Schwartz et al., 2012). The pollen spectra from these sites include *Cathaya*, *Cedrus*, *Tsuga*, which indicate mid-elevations, as well as *Picea* and *Abies* indicating higher elevations, implying that as early as ~30 Ma, a nearby massif attained elevations around 1900 m (1100 to 2900 m according to the minimum and maximum MAT) near Saint-Lions and 1740 m (1100 to 2900 m) near Gambi. Given the configuration of the Oligocene drainage network (Fig. 7), in which both axial and transverse drainages were already established (Grosjean et al., 2012), the high-elevation internal zone of the southwestern Alps, around the present-day Monte Viso, would be the most logical source for these high-altitude pollen.

The Early-Miocene (Aquitainian–Burdigalian) sites of Carros and Le Gour close to Nice (Fig. 1), show the presence of *Cathaya* and

Cedrus (Fig. 6) but insignificant percentages of *Abies* and *Picea*, implying the presence of an elevated massif in the source area during this time, the maximum elevation of which we estimate at 1800 m (Table 1). At present, the most proximal high-elevation massif for these sites is the External Crystalline Argentera-Mercantour Massif (Fig. 1). Using pollen data and quantitative geomorphological studies, Fauquette et al. (1999) showed that the Argentera-Mercantour Massif attained an elevation of ~2000 m during the Pliocene. The exhumation of the Argentera-Mercantour Massif is supposed to start at ~22 Ma (Corsini et al., 2004; Bigot-Cormier et al., 2006; Sanchez et al., 2011); it is therefore unlikely that the massif had already attained such high elevations in the late Early Miocene. An alternative source for pollen grains of microthermic and meso-microthermic plants encountered in Carros and Le Gourg samples would have been northern Corsica and the conjugate Maures-Estérel Massif, as previously suggested by Suc et al. (1992). Apatite fission-track data from northwest Corsica indicate rapid exhumation around 15–25 Ma, attributed to rift-flank uplift in response to Ligurian rifting during the Oligocene–Early Miocene (Zarkhi-Jakni et al., 2004; Danišik et al., 2007).

Several Burdigalian to Serravallian (~21–12 Ma) sites from the Durance Basin (La Rosée, Châteauredon, La Motte d'Aigues) do not record the presence of meso-microthermic and microthermic trees, except *Cathaya* (Fig. 6). Although the ages of La Rosée and Châteauredon overlap the Miocene Climatic Optimum (Jiménez-Moreno, 2005), during which vegetation belts would have risen, our palaeo-elevation estimates correct for this effect and indicate low elevations in the source areas (Table 1). This suggests that, first, the Digne thrust sheet which today overthrusts the Miocene Châteauredon series and develops topography of up to 1000 m in its hanging-wall, had not yet been emplaced at 15 Ma. Second, rivers draining the mountainous hinterland would not yet have reached the marine palaeogulf of the Durance Basin in the Middle Miocene. While the topmost part of the Châteauredon section (Valensole Conglomerates) clearly evidences transport by the palaeo-Durance river, the Middle Miocene sediments do not record alpine clastic inputs. This suggests that the modern Durance drainage network was established in the Late Miocene (Aguilar and Clauzon, 1982).

The analyzed sediments from La Motte d'Aigues post-date the Mid-Miocene cooling. However, the associated lowering of the vegetation belts is not recorded at this distal site. Only the pollen record from the Les Mées borehole encompasses the Mid-Miocene climatic extremes and shows a weak signal of the high-elevation conifers in its upper part (Fig. 6), probably recording their altitudinal descent due to global climatic cooling. Occurrence of high-elevation trees in these pollen records appears mainly controlled by the distance from the pollen source area and the organization of the drainage network.

The proximate early-Langhian Châteauredon and late-Piacenzian Le Rochassas sites bracket emplacement of the Digne thrust sheet and the modern drainage network to between ~15 and ~3 Ma (Hippolyte et al., 2011), as Le Rochassas samples indicate an elevation close to the modern elevation for this site (>800 m; Table 2) and provided a large amount of *Picea* pollen grains (Fig. 6), indicating the proximity of high topography. Likewise, pollen data from Villeneuve-Pigeonnier (Zanclean) show the presence of *Cathaya* among the meso-microthermic trees. *Picea* is present in insignificant percentages and *Abies* is absent (Fig. 6; Table 1). This indicates, that, in contrast to the Burdigalian/Serravallian period (~21–12 Ma), topography between 950 and 1800 m existed in the source area during the Early Pliocene. These results are also in agreement with inferred emplacement of the Digne thrust sheet during Miocene–Pliocene times (Jorda et al., 1988, 1992; Gidon, 1997; Fournier et al., 2008).

Finally, in the Serravallian (~12–13 Ma) La Motte d'Aigues site, located <15 km from the Luberon Massif, the absence of high-

altitude tree pollen grains indicates that the Luberon Massif had not yet attained high elevations at that time. In contrast, high percentages of *Abies* pollen grains (~31%) in the middle Tortonian (~9 Ma) Vaugines site, at the base of the Luberon Massif, show that high topography existed in the source area of this site, which is situated within a syncline filled by Miocene sediments derived from erosion of the Luberon anticline crest (Clauzon et al., 2011). Thus, our data is consistent with structural and topographic development of the Luberon Massif by south-directed thrusting during the time interval 10–6 Ma, as suggested by Clauzon et al. (2011).

The site of Vaugines is today at 430 m elevation, whereas during the middle Tortonian it was near sea level (Table 2). High temperatures during the Miocene (MAT between 10 and 23 °C, MLV around 17 °C) led to a positive shift of around 300 m of the vegetation belts (Table 1). In southern France, the lower altitudinal limit of the *Abies* belt is currently at 1400 m. Therefore, the occurrence of *Abies* in the Vaugines samples indicates source-area elevations above ~1700 m in the Tortonian, while the maximum elevation of the modern Luberon Massif is 1125 m a.s.l. Our results therefore imply that ~600 m surface lowering of the massif by erosion occurred since the Late Tortonian, whereas the foreland was uplifted by ~400 m.

Overall, sites from the western flank indicate the existence of high topography within the internal zone of the southwestern Alps since at least the Early Oligocene, together with outward propagation of deformation and structuring of the foreland during Late Miocene–Pliocene times (Fig. 7). This finding is consistent with the westward migration of the main drainage divide between the Oligocene and Miocene inferred by Jourdan et al. (2012) from provenance data. All Late Oligocene to Miocene sites containing marine deposits are today several hundred meters above sea level, up to 855 m for Gambi. Thus, surface uplift of the western foreland must have taken place during the Neogene and Early Quaternary.

5.3. Evolution of the eastern flank

Late Eocene (~37–34 Ma) clays sampled near Gassino Torinese belong to the Monte Piano Formation of the Torino Hills and are considered as distal Alpine deposits (Festa et al., 2011). The presence of *Cathaya* and the absence of *Abies* and *Picea* in these samples suggest palaeo-elevations of 950 to 1800 m. Jourdan et al. (2013) show that these early deposits in the Torino Hills were derived from the internal western Alps, suggesting the existence of proto-relief in this area already eroded by a palaeo-Dora Riparia drainage system (Fig. 7).

The sites in the Torino Hills that cover the Early to early Late Miocene (Tetti Civera, Rio Civera, Pavarolo, Borelli) indicate high palaeo-elevations of the nearby massifs, from >1680 m (1300–2250 m) during the Aquitanian (~23–20.5 Ma) up to >1925 m (1465–2900 m) during the mid-Tortonian (~10 Ma). Pollen data from Torre Sterpi and Sioneri, covering the latest Messinian (~6 Ma), indicate a minimum elevation around 1800 m (1400–2800 m). However, we interpret this apparent lowering of the minimum elevation of the massif compared to previous periods as an artefact, due to the comparatively colder climate during Pliocene times and associated lowering of the *Abies* vegetation belt.

Thus, our pollen data from the eastern flank of the southwestern Alps suggest continuous high minimum elevations (of the order of 1800 m based on the MLV of MAT), since at least the Early Miocene and possibly since the Late Eocene.

5.4. West–East dissymmetry in topography

Late Paleogene and Early Neogene pollen spectra from the western flank of the southwestern Alps contain relatively high percentages of *Cathaya*, with respect to *Abies* and *Picea*. Likewise, Late

Neogene samples contain relatively high percentages of *Cedrus* and *Tsuga* with respect to *Abies* and *Picea*. Conversely, the sites on the eastern flank show a relative balance between meso-microthermic (*Cathaya*, *Cedrus* and *Tsuga*) and microthermic (*Abies* and *Picea*) tree pollen.

This asymmetry between the two flanks of the mountain belt could be interpreted as a difference in temperature, the eastern flank being cooler than the western one. However, such an interpretation is contradicted by an equivalent abundance of megathermic and mega-mesothermic plants on both flanks (Fig. 6). The different proportions of meso-microthermic versus microthermic tree pollen are better explained by shorter pollen-transport routes from high elevations to the sedimentary sinks towards the east than towards the west, as also observed in the present-day pollen records (Fig. 5).

Pollen data from the western flank imply that the lowest conifer belt, constituted by *Cathaya*, *Cedrus* and *Tsuga*, was close to the sites of deposition and widely developed in space, and that a higher conifer belt constituted by *Abies* and *Picea* was far from these sites. This organization of the vegetation belts supports a relatively progressive increase in elevation on the western flank, as today (Fig. 2B). In contrast, pollen data from the eastern flank imply that both the lower and higher conifer belts were close to the Torino Hills sites, supporting an abrupt increase in elevation on the eastern flank of the southwestern Alps (Figs. 2B, 7). Therefore, the present-day topographic asymmetry of the southwestern Alps dates back to at least the Early Miocene, and possibly to the Oligocene or Late Eocene.

5.5. Topography and exhumation

In many orogenic belts, high topography is associated with high relief and erosion/exhumation rates (Montgomery and Brandon, 2002), as reflected by the present-day topography and exhumation patterns of the western Alps (Vernon et al., 2009). Unfortunately it is impossible to directly determine palaeo-relief from pollen or provenance data. Even though, in theory, detrital thermochronology data may allow information on palaeo-relief to be extracted (Stock and Montgomery, 1996), in practice the data are generally insufficiently resolved to permit this (Beucher et al., 2012; Olen et al., 2012). We know from previously published geo- and thermochronologic data (Bernet et al., 2009; Jourdan et al., 2013) as well as provenance studies (Evans and Mange-Rajetzky, 1991; Jourdan et al., 2012; Schwartz et al., 2012) that, during the Early Oligocene, local peak exhumation rates briefly increased to 1.5–2 km/Myr in the southwestern Alps (Morag et al., 2008; Jourdan et al., 2013), but average long-term exhumation rates remained much lower (~0.3 km/Myr) and fairly constant since ~27 Ma (Bernet et al., 2009). The timing of the peak exhumation rates during the Early Oligocene appears to coincide with the formation of high topography in the southwestern Alps. The slower long-term average exhumation rates would then reflect the persistence of this topography and its asymmetry until today. The westward shift of the southwestern Alps drainage divide during the Oligocene, as proposed by Jourdan et al. (2012) (Fig. 7), and the recent (<2 Ma) glacial modification of high topography in the western Alps (Glotzbach et al., 2013) are superimposed on this overall stable topographic setting.

5.6. Geodynamic implications

Von Blanckenburg and Davies (1995) proposed that in the northwestern and Central Alps slab break-off occurred between 35 and 30 Ma, driving the major and well-documented change from flysch to molasse deposition in the foreland basin at that time (Sinclair, 1997b). The seismic tomography data of Lippitsch

et al. (2003) provide support for a slab break-off event, whereas Duretz et al. (2011) developed a theoretical framework for linking slab break-off and the topographic evolution of the western Alps. These authors state that intermediate slab break-off at the oceanic-continental lithosphere transition causes surface uplift of the overriding plate at a rate of 0.5 km/Myr after ca. 1 Ma, which is partly compatible with the inferences from detrital thermochronology data (Jourdan et al., 2013). Slab break-off followed by surface uplift is synchronous with anticlockwise rotation of the Apulian plate, a change in the convergence direction from south-north to east-west between the Apulian and Eurasian plates, and crustal thickening during continent-continent collision, which all started at about 35–30 Ma (Handy et al., 2010; Malusà et al., 2011; Dumont et al., 2012). This generalized and sharp kinematic change is linked to slab retreat in the nascent Mediterranean realm, inducing strong westward mantle flow beneath the southwestern Alps (Jolivet et al., 2009). However, while slab break-off can account for a general uplift of the Alps during the Early Oligocene, it cannot explain the localized uplift and the dissymmetry recorded at that time in the western Alps.

Theoretical models of doubly-vergent critical wedges (Willett et al., 1993; Whipple and Meade, 2006) predict that the retro-wedge should be steeper than the pro-wedge, consistent with the palaeo-elevation and exhumation record of the southwestern Alps (Carrapa, 2009; this study). Moreover, geophysical analyses of the deep structure of the Western Alps show the presence of the high-velocity, high-density Ivrea body in the core of the orogenic arc, at less than 10 km depth (Schmid and Kissling, 2000; Paul et al., 2001; Lardeaux et al., 2006). The Ivrea body, which is interpreted as a sliver of Apulian mantle, acts as a vertical indenter against the European plate during east-west convergence (Lardeaux et al., 2006). This indenter may have supported localized surface uplift in the internal western Alps and further explain the topographic dissymmetry recorded by sediment provenance (Schwartz et al., 2012; Jourdan et al., 2012, 2013; Fig. 7).

Sites from the western foreland show significant (up to 800 m) surface uplift since the Late Miocene (Section 5.2). Up to 500 m of foreland uplift can be attributed to the flexural isostatic response to increased Quaternary erosional unloading of the western Alps (Champagnac et al., 2008), which would lead to net surface lowering of the mountain range. The remainder could possibly be attributed to deep-seated geodynamic processes, such as renewed slab break-off (Kuhlemann, 2007; Baran et al., 2014), for which geophysical evidence remains scarce, however (Lippitsch et al., 2003).

6. Conclusions

We show that the topography of the internal zone of the southwestern Alps could have reached elevations around 1800 m as early as the Oligocene (~30 Ma). In contrast, the external massifs, including the Mercantour Massif in the southwestern Alps, were uplifted later, during the Late Neogene, while emplacement of the external Digne thrust nappe occurred after the Serravallian (~12–13 Ma). Pollen data show that the present-day topographic asymmetry of the southwestern Alps, with a relatively gentle western flank and much steeper eastern flank, dates back to at least the Early Miocene, and possibly to the Oligocene or Late Eocene.

This topographic evolution is coherent with provenance data and estimates of exhumation rate from detrital thermochronology from the same sedimentary units in the pro- and retro-foreland basins. Rapid surface uplift during the Early Oligocene coincided with a brief episode of rapid exhumation; the high topography of the internal zones of the southwestern Alps has been maintained with moderate long-term average rates of exhumation since that time. Westward propagation of deformation in the Miocene-

Pliocene and Quaternary glacial erosion has not severely perturbed this overall stable system.

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Appendix A. Supplementary material

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.epsl.2014.12.036>.

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Reconstruction of the Northern and Central Apennines (Italy) palaeoaltitudes during the late Neogene from pollen data

Séverine Fauquette^{a,*}, Adele Bertini^b, Vinicio Manzi^c, Marco Roveri^c, Andrea Argnani^d, Elena Menichetti^b

^a Institut des Sciences de l'Evolution (UM2-CNRS 5554), CC 061, Université de Montpellier 2, Place Eugène Bataillon, 34095 Montpellier cedex 5, France

^b Università degli Studi di Firenze, Dipartimento di Scienze della Terra, Via G. La Pira 4, 50121 Firenze, Italy

^c Università degli Studi di Parma, Dipartimento di Fisica e Scienze della Terra, Parco Area delle Scienze 157/A, 43124 Parma, Italy

^d Istituto di Scienze Marine, ISMAR-CNR, Via Gobetti 101, 40129 Bologna, Italy

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ABSTRACT

Palynological studies are considered as an excellent tool for palaeoaltitude estimates as sedimentary basins receive abundant pollen grains from surrounding uplands, especially through riverine detritic inputs. Here, we provide new evidence for estimating the palaeoaltitude of the Northern and Central Apennines (Italy) during the late Neogene (from the late Tortonian to the early Zanclean), based on vegetation data derived from pollen analysis of five sections (Trave, Legnagnone, Cava Li Monti, Maccarone and Stirone). The past vegetation changes reflect shifts in the vegetation belts on the nearby massifs. The climate reconstruction realised on these sites, at sea-level, suggests that mean annual temperatures were higher than today at the end of the Neogene. Therefore, the different vegetation belts occurred at higher elevation than at present to compensate for the higher temperatures. The results obtained in our study suggest that the Northern and Central Apennines were uplifted as early as the Tortonian attaining significant minimum altitudes around 1350 m up to 1500 m at the end of the Miocene in the Central part, a minimum altitude around 1900 m during the Messinian and around 2150 m during the early Zanclean in the Northern part.

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1. Introduction

The Apennines are an active orogenic belt located within the boundary between the African and European plates. Large earthquakes and volcanic activity characterise the Italian peninsula, particularly in the south; the Northern and Central Apennines are affected by frequent earthquakes of moderate magnitude.

The relief history of the Northern Apennines region is a complex coupling between internal (tectonic) and external (e.g. weathering and mass movements) processes. The quantification of palaeoaltitudes remains essential for estimating the uplift rates of mountain belts and for evaluating denudation rates in relation to terrigenous sediments being accumulated in sedimentary basins, as well as for improving palaeoclimatic models (Ramstein et al., 1997; Sepulchre et al., 2009) with independent data.

Palynological studies are considered as an excellent tool for palaeoaltitude estimates. Indeed, sedimentary basins receive, along with detritic inputs from rivers, a high amount of pollen grains; these are representative of all vegetation belts from the catchment area, as demonstrated on modern sediments of the Rhone River (Beaudouin et al., 2005, 2007). In particular, the higher vegetation belts, such as

the belt with fir and spruce, appear useful for estimating the minimum altitude of surrounding mountains.

A method of quantification of palaeoaltitudes based on pollen data has been developed by Fauquette et al. (1999). It takes into account pollen floras accumulated near the coastline providing a regional view of the vegetation from the littoral up to the uppermost altitudinal belts, climatic reconstructions and the relation between latitudinal and altitudinal gradients. This method was successfully applied to early marine Pliocene (5.3 Ma) sediments deposited at the foot of the Mercantour Massif, where it was validated by quantitative geomorphology (Fauquette et al., 1999) and more recently to the Eastern Alps (Jiménez-Moreno et al., 2008), the Pyrenees (Suc and Fauquette, 2012) and the Sila Massif in the Southern Apennines (Fauquette and Combourieu-Nebout, 2013).

The aim of our paper is to use the same method to reconstruct on the base of pollen data, the palaeoaltitude of the Northern and Central Apennines between the end of the Tortonian and the beginning of the Zanclean. Our results can provide constraints on the orogenic evolution of this part of the Apennine belt.

2. Geological settings

The Apennines stretch all along Italy, from Genova (Liguria) to Trapani (Sicily), for 1500 km, showing different geological and morphological

* Corresponding author.

E-mail address: severine.fauquette@univ-montp2.fr (S. Fauquette).

sectors. The Northern Apennines (encompassing Liguria, North Tuscany, Emilia-Romagna) are characterised by relatively low elevations (maximum 2165 m at Cimone Mount), the Central Apennines (encompassing southernmost Tuscany, Latium, Umbria, Marche and Abruzzi) reach higher altitudes up to 2912 m a.s.l. (Corno Grande, Gran Sasso massif) and the Southern Apennines (encompassing Campania, Basilicata, Puglia, Calabria and Sicily) reach 2267 m at Serra Dolcedorme.

The Apennines are one of the youngest mountain belts in the world, and originated during the late Cretaceous to Present convergence between the European and African plates (e.g., Dewey et al., 1989), in a geodynamic setting that was dominated by NW-ward subduction and rollback of the Tethyan oceanic lithosphere with ensuing opening of backarc basins (Malinverno and Ryan, 1986).

In the Northern Apennines the initial stage of oceanic subduction brought to the formation of the Ligurian accretionary wedge, the uppermost nappe of the Apennine stack, which was emplaced tectonically over the basinal sediments of the Tuscan units, deposited on the Adriatic continental margin. Subsequently, the convergence between Adria and the Corsica–Sardinia block, rotating counterclockwise ahead of the Balearic backarc basin, led to a progressive deformation of the units of the Adriatic continental margin (e.g., Argnani, 2012 and references therein). An eastward migrating system of foredeep basins resulted from the soft collision between Corsica–Sardinia and Adria, with the last foredeep basin presently located in the Po Plain and the Adriatic Sea (Ricci Lucchi, 1986; Argnani and Ricci Lucchi, 2001). The Tyrrhenian (internal) side of the Northern Apennines was affected by a regional

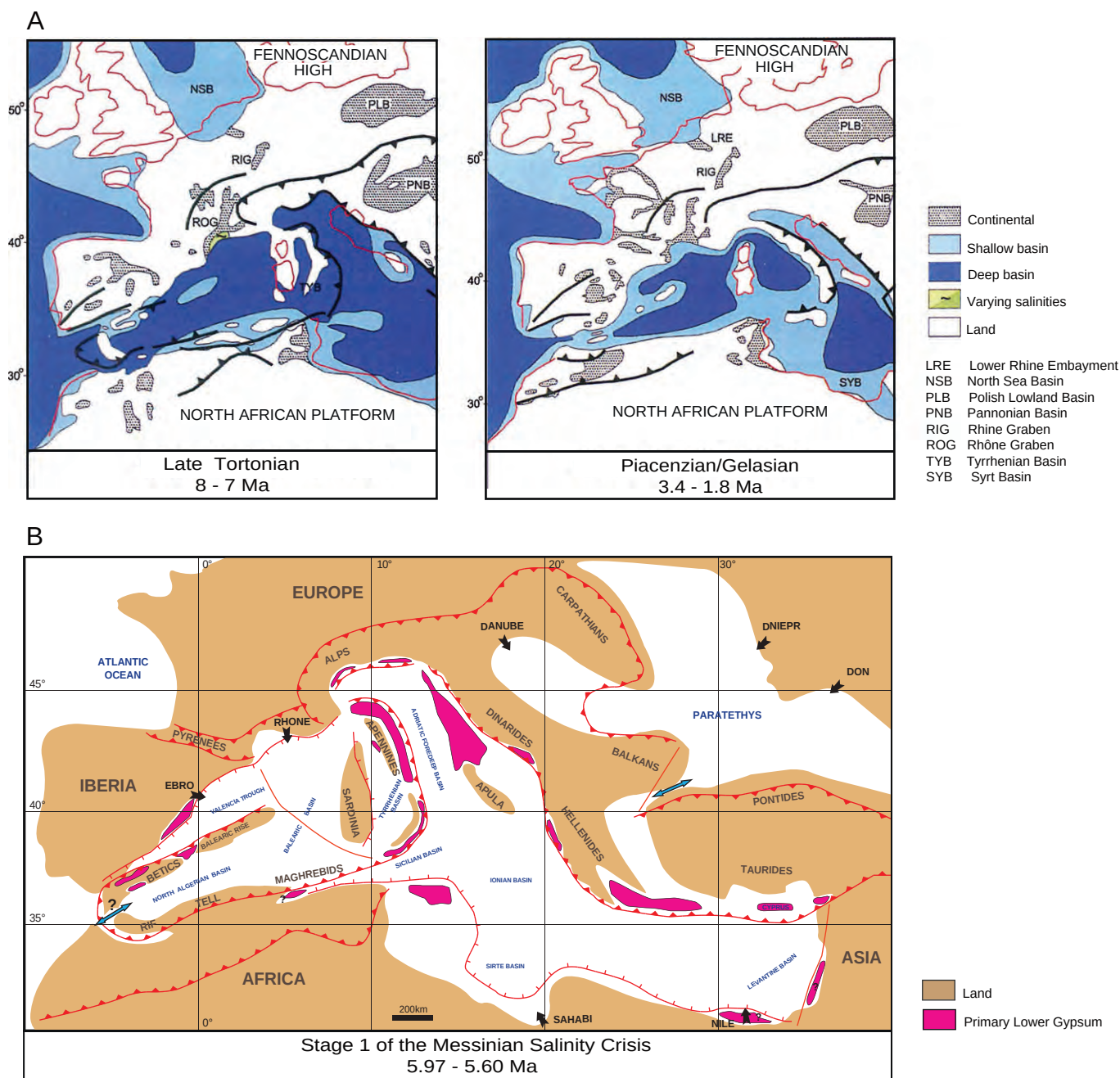


Fig. 1. A. Schematic palaeogeographic maps of the Mediterranean area for the late Tortonian and the Piacenzian/Gelasian showing in particular the emerged part of Italy (modified from Meulenkamp and Sissingh, 2003). B. Schematic palaeogeographic map for the Messinian with the distribution of the shallow (less than 200 m in depth) marginal basins (fuchsia areas) where the Primary Lower Gypsum (Roveri et al., 2008a, 2008b, 2008c, 2008d; Lugli et al., 2010) accumulated during the first stage of the Messinian salinity crisis (5.97–5.60 Ma).

extensional regime in the late Messinian–early Pliocene, with extensional activity decreasing since the early Pliocene (Argnani et al., 2003). On the other hand, small grabens filled by Quaternary sediments characterise the watershed of the Northern Apennines (Bartolini et al., 1982; Argnani et al., 2003).

The retreat–rollback of the west-ward subducted Adriatic slab has been classically proposed to explain the concomitant presence of extensional and compressional features in the Apennines (Malinverno and Ryan, 1986). Several lines of evidence suggest that for the Neogene evolution of the Northern Apennines continental delamination may also play a role (Argnani, 2002; Thomson et al., 2010; Argnani, 2012).

The topographic development of the Northern Apennines is not yet well established. Some authors support a NE-ward migrating crustal orogenic wave, driven by slab retreat, which was active since the late Miocene (Cavinato and De Celles, 1999), implying that a present day-like topography was present since the beginning of orogenic migration. Other lines of evidence indicate that uplift was symmetric across the Apennines and began in the Pliocene, due to a slowdown of slab retreat possibly caused by lithospheric delamination (Carminati et al., 1999; D'Agostino et al., 2001), or slab tear/slab detachment (van der Meulen et al., 1999; Wortel and Spakman, 2000; Gvirtzman and Nur, 2001).

The study of Argnani et al. (2003) supports a two-phase evolution of the Northern Apennines for the Plio–Quaternary. During the early Pliocene, significant horizontal motion occurred, giving rise to extensional basins in Tuscany and on the Tyrrhenian side, and to major thrusting and folding on the Adriatic side. On the other hand, the Pleistocene evolution (after 1 Ma) indicates a predominance of vertical motion, with uplift and widening of the main Apennine range that also involved the Tuscany intermontane basins.

Regional geological data across the Northern Apennines indicate that a substantial change in the tectonostratigraphic regime occurred around the Pliocene–Pleistocene boundary, resulting in a major uplift of the Pliocene deep water sediments that now crop out in the Apennine foothills (Carminati et al., 1999). Moreover, thermochronology data from the internal domain indicate that a uniform erosional exhumation affected both the Apuane and Tuscan nappe since the early Pliocene, suggesting the disactivation of the Apuane extensional fault that previously produced a differential exhumation (Fellin et al., 2007).

Finally, for the scope of this contribution it is interesting to note that at the end of the Neogene, the Africa and Eurasia plates were still subducted to a general northward motion that implies that they were at lower latitudes than today. According to Meulenkamp and Sissingh (2003) the late Tortonian (~8–7 Ma) Europe was ca. 3° in latitude more to the South than today, whereas the Piacenzian/Gelasian Europe was roughly at its modern latitude (Fig. 1A).

Since the middle Miocene to early Pliocene, the Northern and Central Apennines foredeep basin was filled by siliciclastic and evaporitic sediments consisting of four lithostratigraphic units reflecting the structural evolution of the Apennines foredeep (Roveri et al., 2003; Manzi et al., 2007):

- the Marnoso-Arenacea Formation (Langhian–early Messinian) made up of deep water mainly Alpine-derived siliciclastic turbidites that progressively record a more segmented and restricted foredeep (Ricci Lucchi, 1986; Roveri et al., 2003)
- the Gessoso-Solfifera Formation (late Messinian) recording the evaporitic event and the definitive closure of the Miocene foredeep
- the hypohaline Colombacci Formation (latest Messinian) showing the first signals of a Apennines-sourced sedimentation
- the open marine Argille Azzurre Formation (early Pliocene) that represents the marginal deposition, in the inner portion of the Apennines, whereas the main siliciclastic deposits were deposited in the depocentres now buried under the Quaternary alluvial plain deposits.

After relatively stable depositional conditions till the end of the Tortonian, the Apennine foreland system underwent a severe tectonic reorganisation during the Messinian. This led to the closure of the Marnoso-Arenacea foredeep basin, its accretion to the Apennine orogenic wedge and the creation of a new depocentre in a more external position (Manzi et al., 2007). This phase was responsible for the creation of shallow-water silled basins that accommodated the deposition of the primary in situ evaporites (PLG, Roveri et al., 2003, 2008a, b; Fig. 1B) that took place since 5.97 Ma (Manzi et al., 2013) during the first stage of the Messinian salinity crisis (CIESM, 2008; Roveri et al., 2014). At the same time, the deeper basins of the main foredeep experienced the deposition of organic-rich shales (Manzi et al., 2007). During the



Fig. 2. Location map of the studied sites in Northern and Central Apennines (Italy). The detailed stratigraphic sections of the sites are shown in Fig. 3A.

second stage of the MSC, an important tectonic pulse, the so called intra-Messinian phase, produced the uplift and partial emersion of the inner basins, the dismantling of the stage 1 evaporites and their resedimentation in deeper water settings through mass-wasting and gravity flow processes. The third stage of the MSC was a phase of tectonic quiescence that was characterised by a “transgressive”, aggradational stacking pattern of the late Messinian–early Pliocene deposits (Roveri et al., 2008b, c, d).

3. Material and methods

3.1. Pollen data

Selected pollen data of five sedimentary outcrop sections situated in Northern and Central Apennines (Fig. 2) permit to cover the time interval between the end of the Tortonian and the early Zanclean (Fig. 3A and B).

3.1.1. Trave (43°35′0.28″N–13°33′52.53″E, at sea level)

Pollen assemblages document the main palaeovegetational and climatic changes in both the pre-evaporitic (from 7.6 to ca. 6.3) Ma and post-evaporitic (after ca. 5.6 Ma to 5.3 Ma) deposits outcropping in the central sector of the present-day foredeep basin and foreland ramp of the Outer Northern Apennine fold and thrust belt (Iaccarino et al., 2008; Bertini and Menichetti, 2015–this volume). Bisaccate Pinaceae, mostly *Pinus*, show several fluctuations in addition to a progressive decrease, after 7.2 Ma. This is associated to the regressive trend and the deposition of sapropels, before the onset of the MSC. Subtropical (in particular *Taxodium/Glyptostrobus* type and *Engelhardia*) to warm temperate (mainly *Quercus* deciduous type, *Carpinus*, *Juglans*,

Carya and *Ulmus*) arboreal taxa reach the highest percentage values in the sapropels of the upper pre-evaporitic cycles but also in the lower post-evaporitic sequence (p-ev1, Roveri et al., 2001). Herbs show their first significant increase from the upper post-evaporitic sequence (p-ev2; Roveri et al., 2001) with values close to 70% whereas in the underlain deposits they are very poorly represented (never over 10%). Meso- (*Cathaya*, *Cedrus*, *Tsuga*) to microthermic (*Abies*, *Picea*) conifers are also present and sometimes have significant occurrences.

3.1.2. Legnagnone (43°55′10″N–12°21′08″E, 300 m a.s.l.)

The section rests on the allochthonous “Val Marecchia” Ligurian nappe, a portion of the Apennines accretionary prism, which migrated since the early Oligocene on top of the deformed autochthonous Umbro-Marchean-Romagna unit. Its pollen record permits to delineate the main vegetational feature close to the onset of the MSC (Menichetti, 2011; Gennari et al., 2013). The general dominance of the arboreal vegetation indicates a widespread subtropical humid forest type composed of *Taxodium/Glyptostrobus* type, *Engelhardia*, *Myrica*, *Nyssa*, *Sciadopitys*, *Sequoia*, *Distylium*, etc., whereas the generally subordinate occurrence of herbs indicates the absence of severe dry conditions. The most representative group among the arboreal taxa is the *Taxodium/Glyptostrobus*, a typical component of freshwater swamps that shows a mean value of 18.1%. Non-arboreal plants are rare, commonly lower than 5%; nonetheless, they show successive abundance peaks indicating short episodes of relatively drier conditions. Temperate broad-leaved deciduous forest taxa are well represented (in particular *Quercus* deciduous type followed by *Carpinus*, *Juglans*, *Carya*, *Ulmus*, *Zelkova*, *Tilia*, *Pterocarya*, *Liquidambar*) as well as mid to high elevation forest taxa such as *Cedrus*, *Tsuga*, *Abies* and *Picea*.

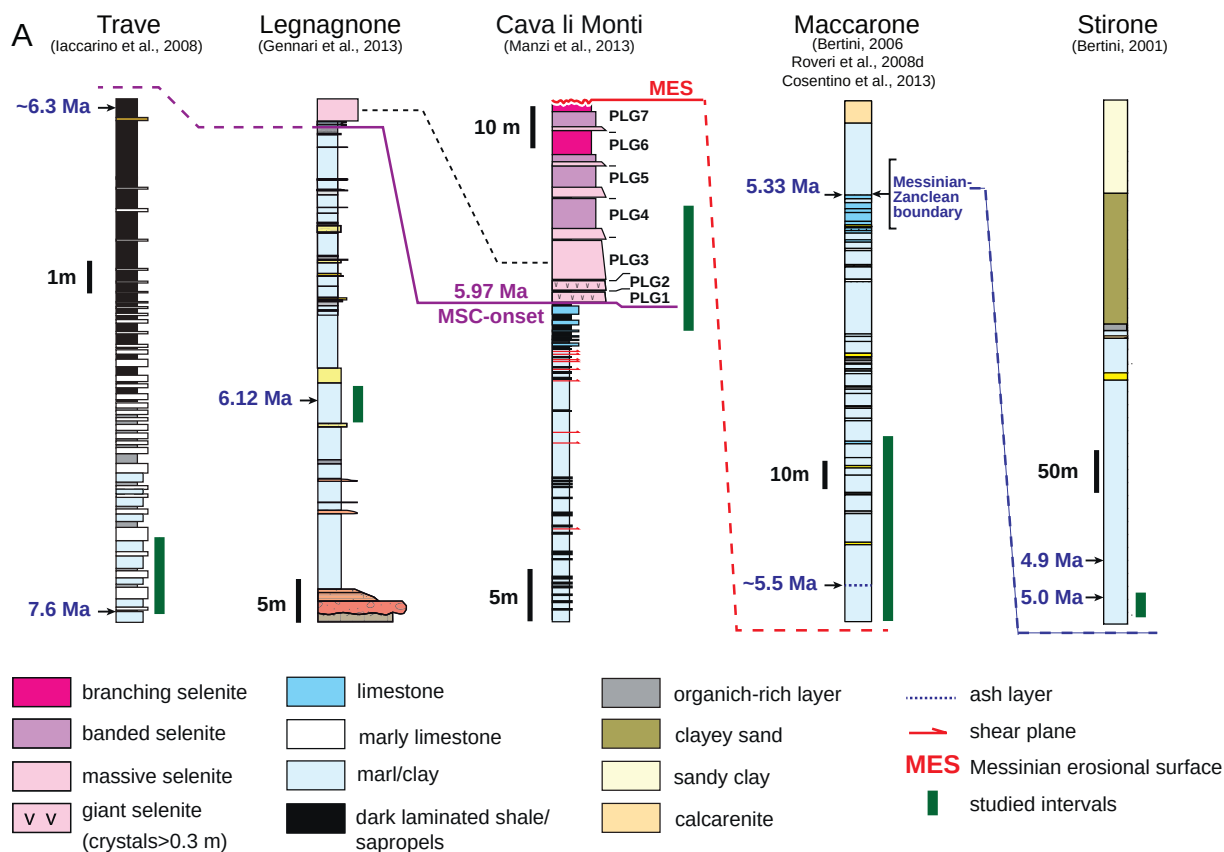


Fig. 3. A. Stratigraphic logs of the five studied sections (modified from Bertini, 2001, 2006; Iaccarino et al., 2008; Roveri et al., 2008d; Cosentino et al., 2013; Gennari et al., 2013; Manzi et al., 2013). B. Summary pollen diagrams and chronologic frame of the studied sites. Abbreviations: p-ev1 and p-ev2, post-evaporitic depositional sequences 1 and 2 (Roveri et al., 2001); PLG, Primary Lower Gypsum; RLG, Resedimented Lower Gypsum (Roveri et al., 2008a); MSC, Messinian Salinity Crisis. Isotopic events on the right of the magnetostratigraphy are from Vidal et al. (2002).

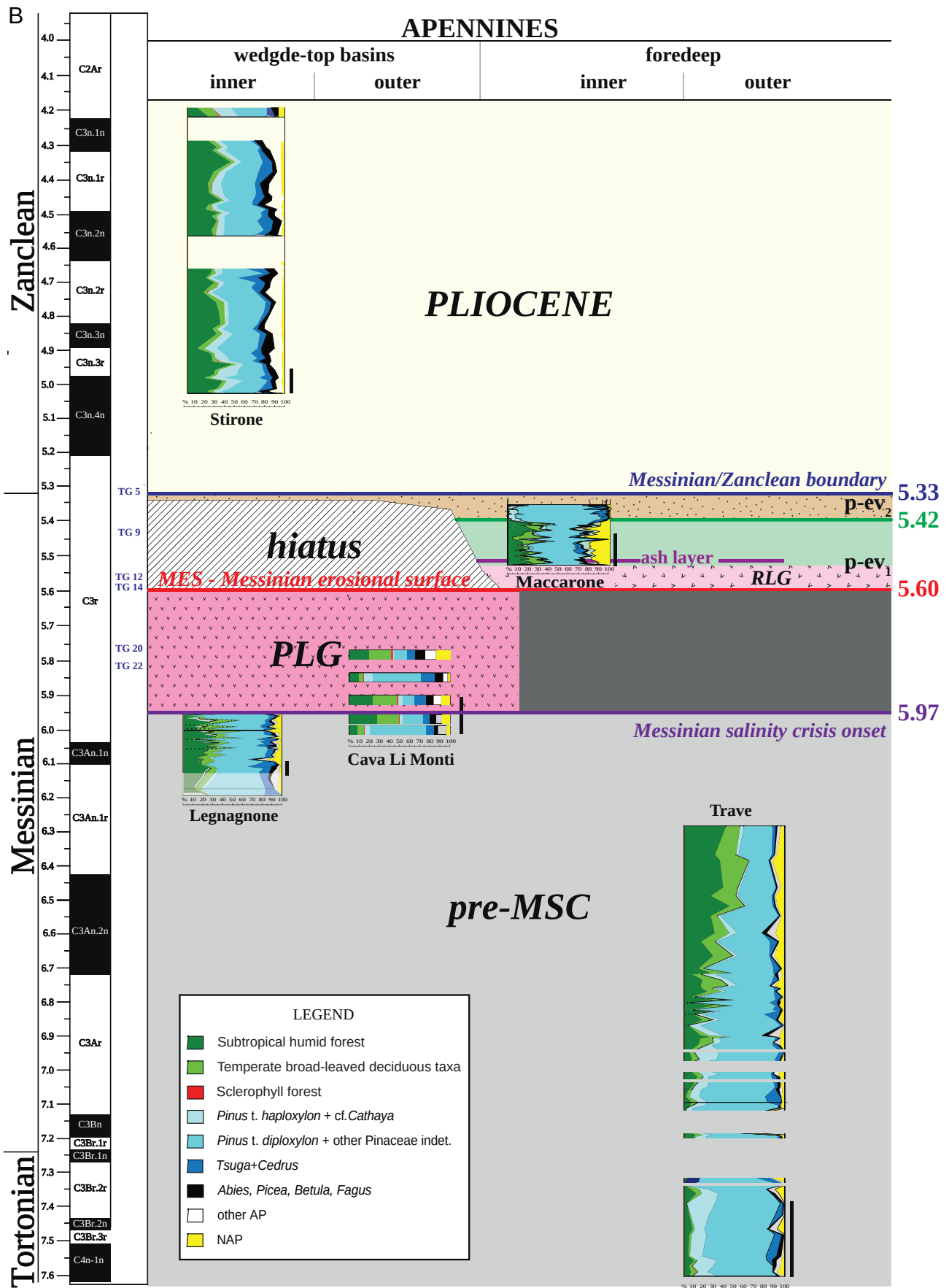


Fig. 3 (continued).

The prevalent humid, subtropical to warm temperate climate was interrupted by some cooling events expressed by the percentage increases of mid to high altitude taxa especially *Abies* and *Cedrus* but also *Picea* and *Tsuga*, and which correlate with glacial isotopic stages 6 and 4 of van der Laan et al. (2005).

3.1.3. Cava Li Monti (43°13'30"N; 11°45'48"E, 246 a.s.l.)

The Cava Li Monti section (CLM), also known in literature as Monticino 1988 (Bertini, 1992, 1994a, b, 2006), belongs to the well-developed Messinian shallow water evaporite sequence, 150 to 170 m thick outcropping in the Vena del Gesso Basin (Vai and Ricci Lucchi, 1977; Manzi et al., 2013). It includes the uppermost part of the pre-evaporitic euxinic shales and the first seven evaporitic cycles of the GS Fm.

Subtropical and warm-temperate plants living under a year-long humid and warm climate (such as *Engelhardia*, *Taxodium*/*Glyptostrobus*, *Myrica*, *Nyssa*) are common and uniformly represented in the upper part of the Marnoso-Arenacea Formation and in the organic-rich shales of the Gessoso-Solfifera Formation. Deciduous forest trees indicative of warm-temperate and temperate climates (*Quercus*, *Carya*, *Ulmus*–*Zelkova*, etc.) are also well represented. The vegetation was typical of a lowland mixed-mesophytic forest. Herbs are rare in the pollen data indicating a dominant forested environment and the absence of dry conditions. Swamp taxa such as *Taxodium*/*Glyptostrobus* type and *Alnus* are well recorded. Mid- to high altitude trees are always fairly well recorded in particular *Cedrus*, *Tsuga* and *Picea*; they show episodic increase phases.

3.1.4. Maccarone (43°24'25"N; 13°6'18" E, 400 m a.s.l.)

The Maccarone section is located in the Marchean outer basin of east-central Italy. Messinian clays and marls with minor sandstones ("p-ev1" and "p-ev2" of Roveri et al., 2001) are overlain by the Pliocene deposits of the Argille Azzurre Formation (Roveri et al., 2008d). U–Pb geochronology on single zircon grains from the volcanic ash layer in the lower part of the section provided an age of 5.5320 ± 0.0046 with sub-precessional resolution (Cosentino et al., 2013).

Humid, subtropical to warm temperate forest taxa generally dominate the pollen assemblages. Tropical plants (*Agave*, *Cordyline*, *Nolina*, *Bombax*, *Canthium* type, etc.) living under warm and moist or dry conditions occur in very low quantities in the lower part of the section (Bertini, 1994a, b, 2006). The open vegetation shows a phase of notable spread in the p-ev1, just above the ash layer. The herbaceous formations are notably marked by the occurrence of *Lygeum*, a modern typical steppe element of northern Africa. Mid to high altitude conifers are well represented all along the Maccarone section, especially in p-ev2.

3.1.5. Stirone (44°50'10.45" N, 9°57'53.95" E, 140 m a.s.l.)

The Stirone section is located in the foothills of the Parma Apennines. It is composed of upper Messinian deposits and Zanclean to Gelasian Argille Azzurre clays. Pollen assemblages (Bertini, 1994a, 2001) indicate the presence of a forested environment during the Zanclean, dominated by subtropical taxa, mainly *Taxodium*/*Glyptostrobus* type, and by broad-leaved taxa such as *Quercus*, *Carpinus*, *Carya*, *Ulmus* and *Zelkova*. Tropical and subdesertic taxa are scarce (e.g. *Nolina*, *Prosopis*, *Sindora*, *Croton*). Herbaceous taxa as well as plants representative of the Mediterranean vegetation are present at low values. Meso- to microthermic taxa such as *Tsuga*, *Cedrus*, *Cathaya* and *Picea* show a progressive increase towards the Gelasian. During the Piacenzian and Gelasian the environment was dominated by the forest but a cooling trend is suggested by the disappearance of tropical taxa and progressive reduction of subtropical taxa. There are also cyclical and rapid changes between thermophilous and meso- to microthermic taxa correlated to the glacial–interglacial cycles of the Northern Hemisphere. Cycles are characterised by the changes between deciduous broad-leaved forest (with *Taxodium*) and mountain coniferous forest

(mainly *Picea*). In contrast to other sites from the Mediterranean area (e.g. Suc et al., 1995a; Bertini, 2010), there is no evidence for a significant expansion of steppe vegetation.

3.2. Palaeoclimate and palaeoaltitude reconstruction

Palaeoaltitude estimates are based on the mean annual temperature at the low altitude allowing the altitudinal and latitudinal temperature gradients to be used (Fauquette et al., 1999). Numerous palynological studies (e.g. Suc et al., 1995a, b, 1999; Jiménez-Moreno, 2005; Bertini and Martinetto, 2011) have shown that the Neogene and Lower Pleistocene vegetation zonation follows a similar latitudinal and altitudinal zonation to that observed in present-day south-eastern China (Wang, 1961), where most of the taxa that disappeared in Europe by the late Neogene may be found. Therefore, high latitude/altitude taxa were excluded from the reconstruction process and the reconstructed climate estimates correspond to the climate at low to middle-low altitude.

The mean annual temperature (MAT) has been reconstructed using the "Climatic Amplitude Method" developed by Fauquette et al. (1998). In this method, the past MAT is estimated by transposing the climatic requirements of the larger modern taxa set to the fossil data. The most likely MAT for a set of taxa is then estimated according to the proper climatic interval for the highest number of taxa. Then, a 'Most Likely Value' (MLV) is calculated. It corresponds to a mean, weighted according to the size of the climatic intervals of all the plants exceeding their threshold. As the precision of the information of these climatic intervals is inversely related to their size, the weights are greater for taxa with smaller intervals (Fauquette and Bertini, 2003).

Vegetation changes according to latitude and altitude, with an almost regular adjustment in respect to decreasing temperatures from lower to higher latitudes in the Northern Hemisphere (Troll, 1966, 1973; Ozenda, 2002). As an example, today the *Abies*–*Picea* vegetation belt occurs between 0 and 500 m altitude in southern Sweden and southern Norway (Noirfalise et al., 1987), but it is situated between 1400 and 2000 m in the southern French Alps (Ozenda, 1961). However, the vertical shift of the vegetation belts in relation to latitude is even more difficult to quantify, as the altitudinal range of plant species is controlled by climatic parameters, as well as by local conditions (nature of soils, slope orientation, etc.). This organisation of the vegetation was used by Ozenda (1975, 1989, 2002) who succeeded in establishing a standard relationship between the latitudinal and altitudinal thermal gradients in Europe, based on average values for the Northern Hemisphere: 0.60 °C per degree of latitude and 0.55 °C per 100 m in altitude. Ozenda (1989) established that a shift of 1 km to the north is equivalent, from a bioclimatic point of view, to a shift in 1 m of altitude. So today, in general, vegetation belts shift 110 m in altitude per degree in latitude.

So, the mean annual temperature estimated from pollen data is transposed into a modern latitude. The difference of latitude between the Neogene site and the modern latitude indicates, using Ozenda's relation, the shift in altitude of the vegetation belts.

High altitude tree taxa represent the best indicators of palaeoaltitude in the fossil pollen spectra. Nevertheless, pollen data do not allow to estimate either the altitudinal range of this vegetation belt or to know whether Alpine herbaceous and perpetual-snow belts existed above. This is due to the difficulty in differentiating Alpine from the lower elevation herbaceous taxa. However, prior to the Pliocene, when climate was tropical to subtropical at the latitude of the Italian peninsula, the minimum estimated palaeoaltitude is relatively well constrained because the uppermost vegetation belt was most likely forested. To estimate the palaeoaltitude, we generally use upper tree line forest species such as *Abies* and *Picea* if they are present. Based on modern pollen spectra from marine sediments close to the Alps (Suc et al., 1999), a threshold value of ~3% for *Abies* and *Picea* has been used to infer past occurrence of *Abies* and *Picea* forests near the sites.

4. Results

4.1. Palaeoclimate

Our climate estimates have been performed on short periods of each pollen sequence in order to reconstruct the climate at a “T” time and not in terms of climate dynamic. The climate has been reconstructed on the sum of only few spectra of each section: on the upper Tortonian spectra of the Trave section, covering the ca. 7.6 to 7.3 Ma time interval, on the sum of three spectra at the base of the Legnagnone section, across 6.12 Ma, corresponding to the end of the Messinian pre-evaporitic phase, on pollen data of the Cava Li Monti section (uppermost part of the Messinian pre-evaporitic/beginning of evaporitic phases, between ca. 6 and 5.9 Ma), on pollen spectra at the base of the Maccarone section corresponding to the lower post-evaporitic phase (between ca. 5.5 and 5.4 Ma) and on the older pollen spectra of the Stirone section corresponding to the Zanclean around 5 Ma.

During the upper Tortonian, the mean annual temperature is estimated between 15.6 and 19.8 °C, with a most likely value (MLV) of 17.5 °C at Trave.

During the Messinian pre-evaporitic phase, the mean annual temperature is estimated between 15.6 and 19.8 °C, with a MLV around 17.8 °C at Legnagnone.

The mean annual temperature at Cava Li Monti (“Monticino 88”) is estimated between 15.6 and 19.8 °C, with a MLV around 17 °C (Fauquette et al., 2006).

During the lower post-evaporitic phase at Maccarone, the mean annual temperature is estimated between 15.9 and 19.8 °C, with a MLV around 17.5 °C (Fauquette et al., 2006).

During the early Zanclean, at Stirone, the mean annual temperature is estimated between 15.9 and 19.8 °C, with a MLV around 17.3 °C.

These estimates illustrate that, during these periods, mean annual temperatures were higher than today, as it was elsewhere in the Mediterranean region (Fauquette et al., 2006, 2007; Jiménez-Moreno et al., 2010).

4.2. Palaeoaltitudes

Palaeoaltitude estimates were calculated using the “Most Likely Values” (MLVs) of mean annual temperatures obtained from pollen data as in Fauquette et al. (1999), Jiménez-Moreno et al. (2008), Suc and Fauquette (2012) and Fauquette and Combourieu-Nebout (2013) and are given in Table 1.

The temperature estimate (MLV = 17.5 °C) at Trave is recorded today at about 37.3°N. Taking into account the palaeolatitudinal position of the site during the Tortonian at around 40.5°N (Meulenkaamp and Sissingh, 2003), the difference is thus ~3.2° in latitude. Using the relationship established by Ozenda (1989), a shift of 3.2° in latitude corresponds to a shift of about 350 m in altitude.

The higher mountains near the current Trave section are the Sibillini Mounts (Vettore Mount: 2476 m). However, in this region, *Abies* is absent due to the deforestation in the last centuries. The existence in the past of this species is only attested by pollen analysis (Marchesoni, 1957, 1958; Paganelli, 1982). Pedrotti (2001) indicates that in the past

the beech wood that formed the montane belt from around 1000 m up to 1800 m also contained *Abies* in its upper part. More to the South, in the Gran Sasso massif, *Abies* appears today from around 1080 m and is well developed around 1300 m (Biondi et al., 2008) that is in accordance with the potential altitude given by Pedrotti (2001) in the Sibillini Mounts. Taking into account the shift of 350 m in vegetation belts between the end of the Tortonian and the present day, *Abies* would have been present above 1350 m and well developed at around 1650 m. This value is an estimate of palaeoaltitude of the lower limit of the *Abies* belt during this period. Accordingly, such a result indicates a minimum altitude for the central part of the Apennines near Trave around 1350 above sea-level during the Late Tortonian.

The temperature estimate (MLV = 17.8 °C) at Legnagnone is recorded today at about 36.8°N. Taking into account the palaeolatitudinal position of the site during the Messinian estimated around 41.5°N, the difference in latitude is thus ~4.7°. That corresponds to a shift of about 500 m in altitude. Today, the lower altitudinal limit for *Picea* forests in the Cimone Mount massif occurs at around 1450 m (Ravazzi et al., 2006). So, during the pre-evaporitic phase of the Messinian, *Picea* would have been present above ~1950 m to compensate for the higher temperatures than today. However, pollen percentages of *Picea* are about 2.2%. This value indicates that *Picea* was present but did not form well developed forests in the mountains close to Legnagnone. So, the palaeoaltitude was less than 1950 m. On the other hand, pollen percentages of *Abies* are about 5.6%. This relatively high value indicates that this vegetation belt was well developed. Today, the lower altitudinal limit for *Abies* forests near Legnagnone (Campigna massif) occurs at around 950 m (Brunetti et al., 2003). So, the lower altitude for *Abies* at that time was around 1450 m above sea-level. Palaeoaltitude of the Apennines near Legnagnone at the end of the pre-evaporitic phase of the Messinian was certainly between 1450 and 1950 m a.s.l.

The temperature estimate (MLV = 17 °C) at Cava Li Monti is recorded today at about 38.1°N. Taking into account the palaeolatitudinal position of the site during the Messinian estimated around 42.5°N, the difference is thus ~4.4° in latitude. That corresponds to a shift of about 480 m in altitude. Pollen grains of *Picea* are well represented in pollen data at Cava Li Monti, around 8.6% as a mean that seems to indicate that this vegetation belt was well developed in the mountains close to Cava Li Monti. Considering the lower altitudinal limit at around 1450 m in the Cimone Mount massif, *Picea* would have been present above ~1900 m. Accordingly, such a result indicates a minimum altitude for the Northern part of the Apennines around 1900 m above sea-level during the Messinian.

The temperature estimate (MLV = 17.5 °C) at Maccarone during the lower post-evaporitic phase is recorded today at about 37.3°N. Taking into account the palaeolatitudinal position of the site during the Messinian estimated around 42°N, the difference is thus ~4.7° in latitude. That corresponds to a shift of about 500 m in altitude. Such a result indicates a minimum altitude for the central part of the Apennines around 1500 m above sea-level.

The temperature estimate (MLV = 17.3 °C) at Stirone during the early Pliocene is recorded today at about 37.6°N. Taking into account a palaeolatitudinal position of the site during the early Zanclean estimated around 44°N, the difference is thus ~6.4° in latitude. That corresponds to a

Table 1
Results of the palaeoaltitude estimates from pollen data.

Section	Age of the analysed interval	Palaeoaltitude (°N)	MAT (°C) Min–MLV–Max	Equivalent latitude (°N)	Latitudinal shift (°N)	Altitudinal shift (m)	Minimum palaeoaltitude (m)
Trave	7.6 to 7.38 Ma (latest Tortonian)	40.5	15.6–17.5–19.8	37.3	3.2	350	1350
Legnagnone	~6.12 Ma (end of the Messinian pre-evaporitic phase)	41.5	15.6–17.8–19.8	36.8	4.7	500	1450
Cava Li Monti	~6 to 5.91 Ma (uppermost part of the pre-evaporitic and lower evaporitic phases)	42.5	15.6–17.0–19	38.1	4.4	480	1900
Maccarone	~5.53 to 5.44 Ma (lower post-evaporitic phase)	42	15.9–17.5–19.8	37.3	4.7	520	1520
Stirone	~5 Ma (early Zanclean)	44	15.6–17.3–19.8	37.6	6.4	700	2150

shift of about 700 m in altitude. Today, the lower altitudinal limit for *Picea* forests in the Cimone Mount massif occurs at around 1450 m (Ravazzi et al., 2006). So, during the early Zanclean, *Picea* high pollen content (8%) indicates the development of a *Picea* forest near the site, which would have been present above ~2150 m. This result indicates a minimum altitude of the massifs of ~2150 m a.s.l. around Stirone.

5. Discussion

Comparison of reconstructed elevations at various times, including the present day, provides information concerning the tendency to the continuing or relaxing uplift process and the importance of erosion of the massifs.

Here, we have used pollen data to reconstruct palaeoaltitudes of the Northern and Central Apennines from the late Tortonian to the early Zanclean.

In our study, the palaeoaltitude estimates were calculated using the “Most Likely Values” (MLVs) of mean annual temperatures obtained from pollen data. The MLVs are certainly less representative of the climate than the entire reconstructed climatic amplitude (as plants may sometimes support large climatic ranges), however they provide a good idea of the optimum climate where they best develop. Moreover MLVs have been statistically tested on modern pollen data and, as a consequence, they are considered to give reliable results (Fauquette et al., 1998).

The method of palaeoaltitude reconstruction is based on the modern distribution of the *Abies* and/or *Picea* belts following the latitudinal and altitudinal thermal gradients. However, the distribution of these taxa is somewhat crude since it depends on several parameters such as exposure to sun, wind, soil, competition and, of course, human activity. *Abies* and *Picea* could certainly develop at lower altitudes under favourable environmental conditions. Moreover, palaeoaltitudes estimated are the minima as pollen data do not allow establishment of the altitudinal range of the *Abies* or *Picea* belts, or whether the alpine herbaceous and perpetual-snow belts above it existed.

For a long period of time, extending at least up to the Tortonian and locally the early Messinian, the source area for the largest part of the sediments that filled up the Apennine foredeep was located in the Alps (Ricci Lucchi, 1986; Argnani and Ricci Lucchi, 2001). When and where the transition from an Alpine- to an Apennine-fed foredeep occurred is not clearly defined, for two reasons: i) due to the Apennine thrust-belt and foredeep migration towards the East, the reduction of the Alpine contribution was not uniform in all of the foredeep sub-basins, but started first from the western ones that were in a more elevated position; ii) the first Apennine-sourced sediments recycled older Alpine-sourced deposits (Ricci Lucchi, 1986; Argnani and Ricci Lucchi, 2001; Lucente et al., 2002).

However, some authors (Ricci Lucchi, 1986; Argnani and Ricci Lucchi, 2001; Cibi et al., 2001) argued for a “feeding inversion” from Alpine to Apenninic sources of sediments during the Upper Miocene, driven by a tectonic phase possibly culminating during the Messinian (the intra-Messinian tectonic pulse).

The results obtained in our study tend to indicate that Northern and Central Apennines were uplifted as soon as the late Tortonian. It seems that they were attaining significant minimum altitudes ranging from 1350 m to 1500 m at the end of the Miocene in the Central part (Sibillini Mountains?) and a minimum altitude around 1900 m during the Messinian and around 2150 m during the early Zanclean in the Northern part (Cimone Mount?). For the central part, Sadori et al. (2010) record in late Pliocene continental deposits of the high Salto river valley (Borgorose) the contemporary presence of taxa living at different altitudes (in particular high percentages of *Picea*) suggesting that the Apennine chain was already playing an important role in the vegetation distribution.

As described by Bertini (2001) and Bertini and Martinetto (2011), past vegetation was, as today, organised in altitudinal belts on the slopes

of mountainous massifs, following the thermic and precipitation gradients. So, the presence of microthermic taxa implies the existence of significant relief near the studied sites. But no information may be given, using pollen data, on the location of these mountains. For instance, the palaeoaltitude estimate based on pollen data of Legnagnone, covering the end of the pre-evaporitic phase of the Messinian, indicates a minimum altitude of 1450 m for massifs uphill from the site. However, Benvenuti (1997) and Balestrieri et al. (2003) indicate that little or no topography was present between 5 and 2 Ma at Monte Falterona, the nearest mountain to Legnagnone. Our result could thus correspond to the palaeoaltitude of the Cimone Mount region.

At Maccarone, pollen percentages of microthermic plants (*Picea* and in particular *Abies*) are lower than at Trave, although these two sites are situated in the same region and that the temperature estimates at low altitude are equivalent. This is certainly due to the palaeoenvironmental conditions where the pollen grains deposited. At Trave during the late Tortonian, the flora (high pollen percentages of *Pinus* for instance) point out open marine conditions whereas the base of the Maccarone section corresponding to the lower post-evaporitic phase shows a flora indicating neritic to marginal marine conditions (Bertini, 2006). These palaeoenvironmental conditions that are confirmed by dinocyst assemblages recorded in the sequences (respectively Bertini, 2006; Iaccarino et al., 2008), may explain the differences in the bisaccate pollen grains (*Pinus*, *Abies*, *Picea*).

In the Stirone section, Bertini (2001) attributes the presence of microthermic taxa (*Picea*, *Abies*) to mountainous massif northward (Alps, PreAlps). However, following Ricci Lucchi (1986) and Cibi et al. (2001), the source of sediments may be the Northern Apennines at that time. Moreover, high sedimentation rates during the Lower Pliocene, reaching 104 cm/kyr at Stirone and allowing the deposition of nearly 300 m of “Argille azzurre” in less than 0.5 Ma (Channell et al., 1994), imply the existence of significant relief submitted to intense erosion nearby. The estimated palaeoaltitude could thus reflect the Apennines rather than the Alps and more particularly the Parma Apennines. The palaeoaltitude estimated at Stirone may appear high, but looking at Legnagnone or Trave palaeoaltitude estimates, the result is relatively homogenous.

According to Ventura et al. (2001) the exhumation of the Apennines possibly started at 14 Ma, but more convincing data about rock cooling indicate a younger age between 10 and 8 Ma. However, understanding how the palaeoaltitude can be related to exhumation history is difficult to assess, also because pollen data only reflect surface elevation (England and Molnar, 1990). The concomitant occurrence in late Tortonian of rock exhumation, indicated by thermochronology data, and surface elevation, suggests that processes causing crustal thickening dominated. For these initial stages of the evolution thrust stacking within the growing Apennine belt appears the most likely candidate.

Our results indicate that creation of high reliefs in the Apennines occurred by late Tortonian. This does not necessarily mean that the crustal wave model is to be preferred; in fact, in the complex evolution of the Northern Apennines both NE-ward migrating crustal waves and post early Pliocene symmetric uplift can have occurred. The former may have operated in the earlier stages, when slab retreat was mostly active, whereas the latter acted when slab retreat came to a slowdown, likely due to the thick continental crust of Adria entering subduction (e.g., Argnani, 2012). Mantle dynamics can also contribute to create the post early Pliocene symmetric uplift (D’Agostino et al., 2001). Moreover, recent thermochronology data suggest that marked along-strike variations in collisional wedge dynamics, from slab retreat and frontal accretion to underplating and cessation of retreat, can occur at the scale of the Northern Apennines (Thomson et al., 2010).

6. Conclusion

Palynological studies are considered as an excellent tool for palaeoaltitude estimates as sedimentary basins receive abundant pollen grains

from surrounding uplands, especially through riverine detritic inputs. The palaeovegetation, palaeoclimatic and palaeoaltitude reconstructions from the late Tortonian to the early Zanclean based on vegetation data derived from pollen analysis of five sections of Central and Northern Apennines (Trave, Legnagnone, Cava Li Monti, Maccarone and Stirone) indicate that:

- 1) Past vegetation changes recorded in pollen data reflect shifts in the vegetation belts of the nearby massifs.
- 2) Mean annual temperatures at sea level were higher than today, which is consistent with previous climate reconstructions from other Mediterranean sites. Therefore, the different vegetation belts occurred at elevation higher than at present to compensate for the higher temperatures.
- 3) Northern and Central Apennines were uplifted as early as the late Tortonian, attaining significant minimum altitudes ranging from 1350 m to 1500 m at the end of the Miocene in the Central part, and a minimum altitude around 1900 m during the Messinian, and around 2150 m during the early Zanclean, in the Northern part.

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The Alps: A geological, climatic and human perspective on vegetation history and modern plant diversity

Séverine Fauquette¹, Jean-Pierre Suc², Frédéric Médail³, Serge D. Muller¹, Gonzalo Jiménez-Moreno⁴, Adele Bertini⁵, Edoardo Martinetto⁶, Speranta-Maria Popescu⁷, Zhuo Zheng⁸ and Jacques-Louis de Beaulieu³

¹ *Institut des Sciences de l'Evolution, Université de Montpellier, CNRS 5554, IRD, CC 065, Place Eugène Bataillon, 34095 Montpellier cedex 5, France*

² *Sorbonne Universités, UPMC Univ. Paris 06, CNRS, Institut des Sciences de la Terre Paris (iSTeP), 4 place Jussieu, 75005, Paris, France*

³ *Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix Marseille Université / CNRS / IRD /AU. Campus Aix-Technopôle de l'Environnement Arbois-Méditerranée, 13545 Aix-en-Provence cedex 4, France*

⁴ *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Fuente Nueva S/N, 18002 Granada, Spain*

⁵ *Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira, 4 50121 Firenze, Italy*

⁶ *Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, 10125 Torino, Italy*

⁷ *GeoBioStratData.Consulting, 385 route du Mas Rillier, 69140 Rillieux la Pape, France*

⁸ *Department of Earth Sciences, Sun Yat-sen University, Guangzhou 510275, China*

Author for correspondence (*): severine.fauquette@umontpellier.fr

Abstract

Mountain ecosystems, and in particular European Alpine ecosystems, have a rich biodiversity as they represent complex associations controlled by elevation, soils and rocks, and climatic conditions following latitude, longitude, slope orientation and aspect. Vegetation belts are organized with respect to altitude according to a concomitant decrease in temperature and increase in precipitation, and are defined by their dominant plant elements. Plant diversity within the Alps also results from these mountains' location at the transition point between cold-temperate and warm-temperate climates and from their historical biogeography. In order to explain how past environmental changes have shaped the modern plant diversity and the organization of vegetation in altitudinal belts, a temporal dimension may be provided by palaeovegetation data. Abundant micro- (pollen) and macro-remains (leaves, fruits, seeds) show that European Cenozoic vegetation exhibits a similar latitudinal and altitudinal organisation to the vegetation belts observed today in south-eastern China where most of the taxa, missing in Europe since the late Neogene, now occur. Late Eocene to Pliocene pollen floras of the south-western and Eastern Alps are characterized by the presence of megatherm plants and an abundance of mega-mesotherm plants. These are typical of moist evergreen low altitude forests, and characterized by the presence of *Cathaya*, a conifer now restricted to subtropical China at mid to high elevations. Pollen data indicate the presence of *Abies/Picea* forests at high altitudes since at least the Oligocene. Since then, several thermophilous taxa have declined, and some of them have disappeared from the Alps due to natural or human-related processes that are responsible for the modern plant diversity pattern there. These processes include the uplift of the mountain range, which began ~35 Ma, late Neogene global cooling, Pleistocene glacials/interglacials and more recent human impact.

Keywords: Palaeo-phytogeography, Pollen, Mountain uplift, Palaeoaltitude, Cenozoic, Global cooling, Climatic cycles

x.1 Introduction

Mountain vegetation is characterized by the altitudinal stratification of plants related to temperature and precipitation. Vegetation zones change from low to high latitude or from low to high altitude in the same way (Ozenda 1989): the replacement of taxa occurs as vegetation types adapt to colder conditions.

Mountain plant ecosystems generally have high diversity as they represent complex assemblages influenced by elevation, climatic conditions—which follow the latitude and longitude—and variable amounts of rainfall. Moreover, the physiographic complexity of mountains creates environments that can vary over short distances due to, for instance, exposure to sun or slope angle and aspect.

In the Alps, vegetation organization is also complex because of the large size of the mountains and their position at the crossroads of many floristic provinces (Ozenda 2009). Moreover, the Alpine arc is oriented north/south in France but west/east for the rest of the chain (Figure x.1a). The French section of the chain is thus characterized by important differences between the southern and the northern parts, with the Southern European Alps being drier as they are under Mediterranean influences.

Plant diversity within the Alps mainly results from their location at the transition point between cold-temperate and warm-temperate climates, their landscape heterogeneity, the local climate variability that arises from complex topographies and historical biogeography. A detailed knowledge of the past is thus essential for a better understanding of the processes that have controlled changes in plant diversity up to the present.

This chapter, which focuses primarily on the Western Alps, starts with a description of the present flora and vegetation patterns in their physiographic and geological context. Then it shows how the intense tectonic activity in this region over the last 40 My has influenced the flora and vegetation. Finally, it shows the role of Pleistocene climatic cycles and human impact on the mountains and their flora.

x.2 Present flora and vegetation patterns in the physiographic, climatic and geological context of the Alps

x.2.1 Plant distribution and endemism patterns

The European Alps are one of the most important hotspots of plant biodiversity in Europe (Ozenda 1985, 2002), with a high number of endemic taxa. According to *Flora Alpina* (Aeschimann et al. 2004), the Alps encompass 3983 indigenous taxa of vascular plants, which is more than one-third of the total European flora. The average taxonomic richness of the Alps is estimated at about 2200 taxa per 10,000 km², and despite their relatively restricted area, the Southwestern Alps are home to more than 70% of the entire Alpine flora. In the Alps, 501 endemic taxa are registered, making up 4% of the European flora. This corresponds to an endemism rate of 12.6% within the area's native flora.

The distribution of endemics (Figure x.1a) is mainly concentrated in the southernmost Western Alps and the southern part of the East Eastern and West Eastern Alps (Noble & Diadema 2011). At the junction of the Mediterranean Basin and the Alps, the Maritime and Ligurian Alps constitute a zone of geographic overlap between major biotic assemblages (Comes & Kadereit 2003), an important hotspot of plant biodiversity (Médail & Quézel 1997) and also a major refugium (Médail & Diadema 2009; Figure x.1b). This region, with 25% of the endemic plants of the whole range, represents one of the most important biogeographical areas in Europe due to the high concentration of palaeoendemic and endemic plants (Casazza et al. 2008; Noble & Diadema 2011). Recent molecular investigations of endemic plants from

the Maritime and Ligurian Alps show that vicariance events are the most important factor explaining the distribution and genetic patterns of plant populations there (Casazza et al. 2013). The Maritime Alps do not act as a strong barrier to the migration of plants, and moderate gene flow seems to create an admixture between some plant populations, even when separated by deep valleys (Diadema et al. 2005). The persistence of several endemics throughout various glacial periods appears to be linked to the capacity of mountains to provide a wide diversity of microhabitats within a reduced space.

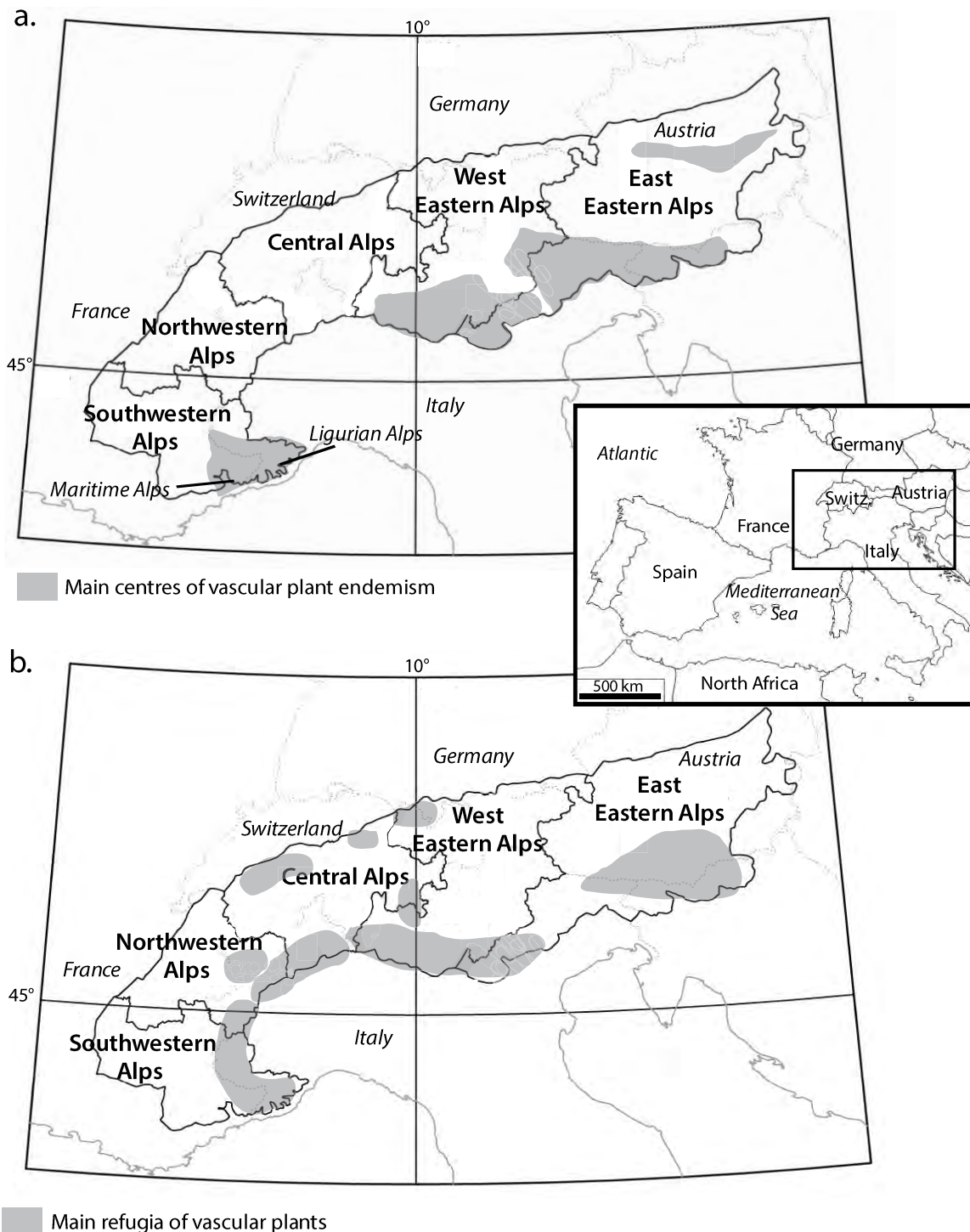


Fig. x.1. The main centres of vascular plant endemism (a) defined by Noble and Diadema (2011) and the main refugia of vascular plants (b) in the Alps defined by Schönschwetter et al. (2005), placed on map modified after Aeschimann et al. (2011), which presents the five main phytogeographic zones of the Alps.

In the Alps and Carpathian Mountains, species richness and genetic diversity do not co-vary for mountain vascular plants (Taberlet et al. 2012); rather, genetic diversity is associated with the glacial and post-glacial history. In the Alps, genetic rarity (the presence of rare alleles or restricted haplotypes) is correlated with both species rarity (i.e. rare markers tend to be located in the same areas as rare species) and species endemism (i.e. rare markers in widespread species tend to be situated in the same areas as endemic species). Rare markers are often fixed in long-term isolated refugial populations, and these crucial areas correspond to distinct glacial refuges in which the highest endemism levels also occur (Schönswetter et al. 2005).

x.2.2 Vegetation

Vegetation belts (also called altitudinal zones) in the Alps are well-characterized by bioclimatic factors and their principal vegetation types, especially forests. Vegetation belts are organized altitudinally according to steep ecological gradients with a concomitant decrease in temperature and increase in precipitation, extending from the lowlands to the nival zone. In the Central Alps, five vegetation belts are distinguished: the collinean, mountain, subalpine, alpine and nival belts (Table x.1).

Table x.1. Structure of the vegetation belts of the Alps in relation to the mean minimum temperatures of the coldest month of the year (m), and their correspondence with two concepts of the Mediterranean vegetation belts.

m (°C)	Alpine vegetation belts		Mediterranean vegetation belts	
	Ozenda 1985	Main vegetation types	Ozenda 2002	Quézel and Médail 2003
-10 -9	Nival	Bryophytes and lichens		
	Alpine	Grasslands with Poaceae and Cyperaceae; low heathlands with <i>Salix</i> , <i>Juniperus</i> , <i>Vaccinium</i>	Alti-Mediterranean	Oro-Mediterranean
-7 -6	Subalpine	Coniferous forests with <i>Picea abies</i> , <i>Larix decidua</i> , <i>Pinus mugo</i> , <i>Pinus cembra</i>	Mountain-Mediterranean	Mountain-Mediterranean
-4 -3	Mountain	Forests with <i>Fagus sylvatica</i> and/or <i>Abies alba</i> ; mesophilous forests with <i>Pinus sylvestris</i>	Supra-Mediterranean	Supra-Mediterranean
-1 0 1	Collinean	Deciduous forests with <i>Quercus pubescens</i> , <i>Q. robur</i> or <i>Q. petraea</i> ; xeric forests with <i>Pinus sylvestris</i> ; mesophilous forests with <i>Tilia</i> , <i>Fraxinus</i> , <i>Acer</i> , <i>Prunus</i> .	Medio-Mediterranean	Meso-Mediterranean
		Mediterranean vegetation in SW Alps (southern slopes)	Per-Mediterranean	Thermo-Mediterranean
				Infra-Mediterranean
9 10 > 10				

In the Southwestern Alps, vegetation is similarly organized in altitudinal belts on both flanks of the mountains but with more pronounced Mediterranean influences occurring on the southern slopes, from the lowest thermo-Mediterranean to the oro-Mediterranean belt, which corresponds to the alpine belt of the Central Alps (Table x.1). These southern mountains are heterogeneous from a biogeographical viewpoint, with the southern side clearly influenced by Mediterranean elements whereas the northern side is composed of medio-European vegetation

(Barbero & Quézel 1975). The altitudinal limits of these vegetation belts vary along a latitudinal gradient, but are ~700 m wide in vertical elevation (Ozenda 1989). For collinean to subalpine species, especially trees, temperature often represents the limiting factor for survival at the upper limit, and moisture at the lower limit.

These vegetation belts are well delimited by modern pollen data collected from moss pollsters along two transects across the Southwestern Alps (Fauquette et al. 2015; Figure x.2). In order to reconstruct Cenozoic vegetation and climate information from pollen data, these authors established the relationship between modern pollen data and vegetation to serve as a baseline.

To create this reference dataset, pollen grains were grouped according to vegetation belts. However, *Pinus* was separated because its pollen is not identifiable at the species level and may be representative of several vegetation belts. Pollen grains of *Larix* are scarce; samples containing this genus were collected within its forests or from sites immediately below such forests. Pollen grains of Cupressaceae are grouped together because infra-family identification (genus identification) is impossible, even though their species grow at different altitudes in the Southwestern Alps: *Cupressus sempervirens*, *Juniperus oxycedrus* and *J. phoenicea* in the two lowermost Mediterranean vegetation belts; *J. thurifera* in the higher supra-Mediterranean belt and in the lower part of mountain-Mediterranean belt; and *J. communis* and *J. sabina* in the mountain-Mediterranean belt. Most of the herbaceous pollen grains cannot be distinguished at the genus level, whereas such plants can inhabit different altitudes; their abundance may indicate open and/or undergrowth vegetation. Finally, alpine tundra-like plants (*Aconogonum alpinum*, *Gentiana*, *Centaurea uniflora*) were identified in only a few sites.

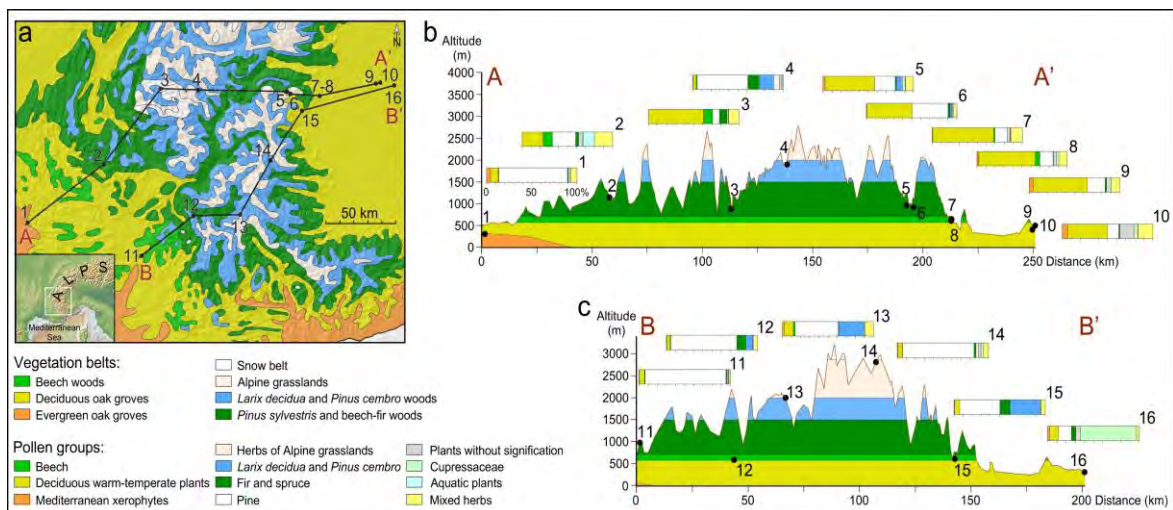


Fig. x.2. Relationship between vegetation belts positioned on a topographic profile (Noirfalise et al. 1987; Ozenda 2002) and modern pollen data collected from moss pollsters along two transects (modified from Fauquette et al. 2015). (a) Simplified vegetation map of the Southwestern Alps (from Noirfalise et al. 1987) on which the transects are shown (dots correspond to the moss pollsters). Pollen localities and altitudes are indicated below. (b) Transect AA': 1, Nyons (300 m); 2, Luz la Croix haute (1100 m); 3, Le Freney (800 m); 4, Col du Lautaret (1850 m); 5 - 6, Pinerolese (Lago Villaretto di Roure and Balma di Roure, 980 and 890 m, respectively); 7 - 8, Cumiana Giaveno (612 and 605 m, respectively); 9 - 10, Baldissero Torinese (Val Samfrà and Superga road, 383 and 537 m, respectively). (c) Transect BB': 11, Taulanne (995 m); 12, Sisteron (540 m); 13, Saint-Léger (2000 m); 14, Agnel (2800 m); 15, Pinerolese, Inverso Pinasca (560 m); 16, Moncucco Torinese, Borelli (315 m).

These west-east transects show that there is a good correlation between pollen data and observed vegetation distributions along altitudinal and longitudinal gradients and that the vegetation distribution follows a clear asymmetric topography (Figure x.2): replacement of pollen groups as elevation increases appears progressive on the western flank, but much more abrupt in the east.

Pollen data may therefore be used to reconstruct Paleogene to Quaternary palaeovegetation. Moreover, for these periods, information from pollen may be complemented by macrofossils when available in the same region. However, these fossils are produced from plants that lived not more than a few kilometres away from the fossilization site and rarely record plants growing in the higher belts. To get around this problem, Bertini and Martinetto (2011) used the presence of pollen and the concomitant absence of macrofossils in several deposits of the same age to pinpoint those plants that probably grew at higher elevations (e.g. *Cedrus*, *Picea*, *Tsuga*).

x.3 Vegetation history of the Alps since the late Eocene

The Alps resulted from the convergence of the European and African plates, trapping the Apulian microplate between them, which resulted in the closure of the Tethys Ocean by the Eocene, followed by a collision between the European and Adriatic plates (e.g. Rosenbaum & Lister 2005). This complex collision history led to a nappe stack involving basement and cover rocks of the European margin, of the intervening ocean and micro-continents, and of the Adriatic margin.

The intense tectonic activity in this region over the last 40 Myrs has influenced the vegetation and flora, with the appearance of high mountains and new marine basins and the consequent landscape fragmentation, environmental heterogeneities and new climatic patterns.

x.3.1 Vegetation history before human impact

Abundant pollen records (e.g. Suc 1989; Suc et al. 1995; Jiménez-Moreno et al. 2005, 2010; Bertini 2010) show that European Neogene vegetation followed belts that were aligned similarly in latitude and altitude to the belts seen today in south-eastern China (Wang 1961), where most of the taxa that disappeared from Europe by the late Neogene are still extant.

The study by Fauquette et al. (2015) shows that in the Southwestern Alps, late Eocene to Pliocene pollen floras (Figures x.3, x.4; Fauquette et al. 2015) are characterized by prevalent mega-mesotherm plants (see the definitions of these plant groups in the legend of figure x.4) reflecting subtropical conditions, and sometimes high frequencies of *Cathaya*, a conifer restricted today to subtropical China at mid to high elevations, below the *Abies* and/or *Picea* belts (Wang 1961). Pollen records suggest that the past representatives of *Cathaya* in Europe probably occupied a similar ecological niche (e.g. Suc 1989; Combourieu-Nebout et al. 2000, 2015; Biltekin et al. 2015). Megatherm plants supporting an interpretation of tropical conditions were present in all of the Eocene to mid-Miocene samples (Figure x.4). The maximum frequency of such species occurred during the early Langhian (~15 Ma; Jiménez-Moreno et al. 2005), corresponding to the mid-Miocene Climatic Optimum (MCO). The pollen record of mega-mesotherm plants decreases from the early Zanclean (~5 Ma) to the Piacenzian (3.6–2.6 Ma), and major disappearance events have occurred since the earliest Pleistocene (2.6 Ma), due to the onset of Northern Hemisphere glaciations (Suc 1984; Bertini 2010). Climate gradients linked to latitude, altitude and physiography of pollen sites explain the different timing of the extinctions of *Taxodium*-type, *Cathaya* and *Tsuga* species, among others (e.g. Suc et al. 1995; Bertini 2010).

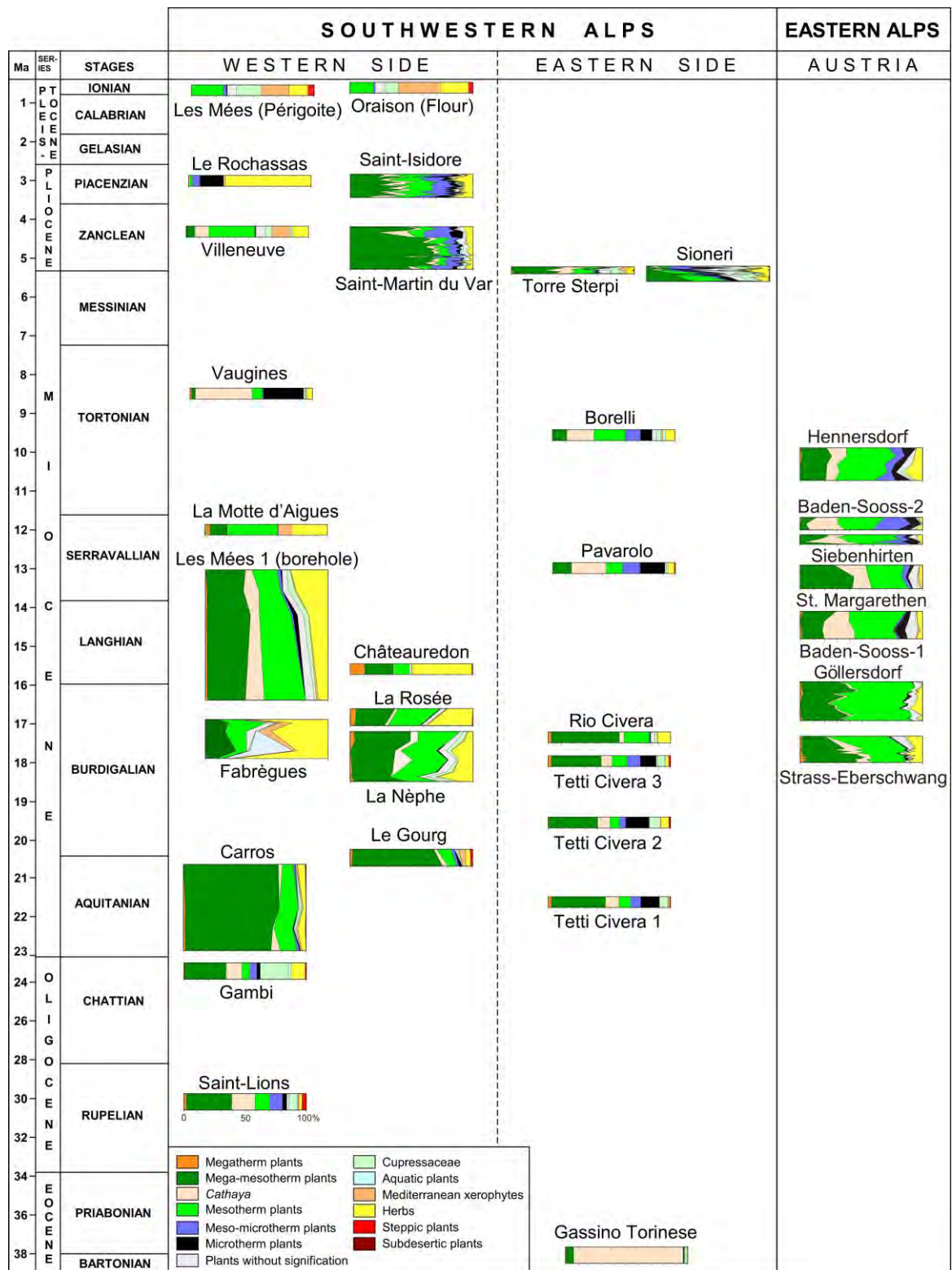


Fig. x.3. Synthetic pollen diagrams from late Eocene to Pleistocene localities of the Southwestern and Eastern Alps and their position in a chronostratigraphic frame. Note the change of timescale at the Paleogene/Neogene boundary. Taxa have been arranged into 13 different groups (*Pinus* excluded) based on ecological criteria to visualize the main changes in the palaeovegetation cover. Plants without signification indicates families (e.g., Rosaceae, Ranunculaceae, Rutaceae) in which pollen identification is difficult at the genus level and comprises cosmopolitan taxa and/or taxa with wide ecological requirements, plus unidentified pollen grains. Some groups are classified according to thermic requirements with respect to the Nix (1982) classification: equatorial and tropical forests are inhabited by megatherm plants ($MAT > 24^{\circ}\text{C}$), subtropical forests by mega-mesotherm plants ($20^{\circ}\text{C} < MAT < 24^{\circ}\text{C}$), temperate deciduous forests by mesotherm plants ($14^{\circ}\text{C} < MAT < 20^{\circ}\text{C}$), boreal coniferous forests successively by meso-microtherm ($12^{\circ}\text{C} < MAT < 14^{\circ}\text{C}$) and microtherm ($MAT < 12^{\circ}\text{C}$) plants and tundra by microtherm plants (modified from Fauquette et al. 2015 and Jiménez-Moreno et al. 2008).

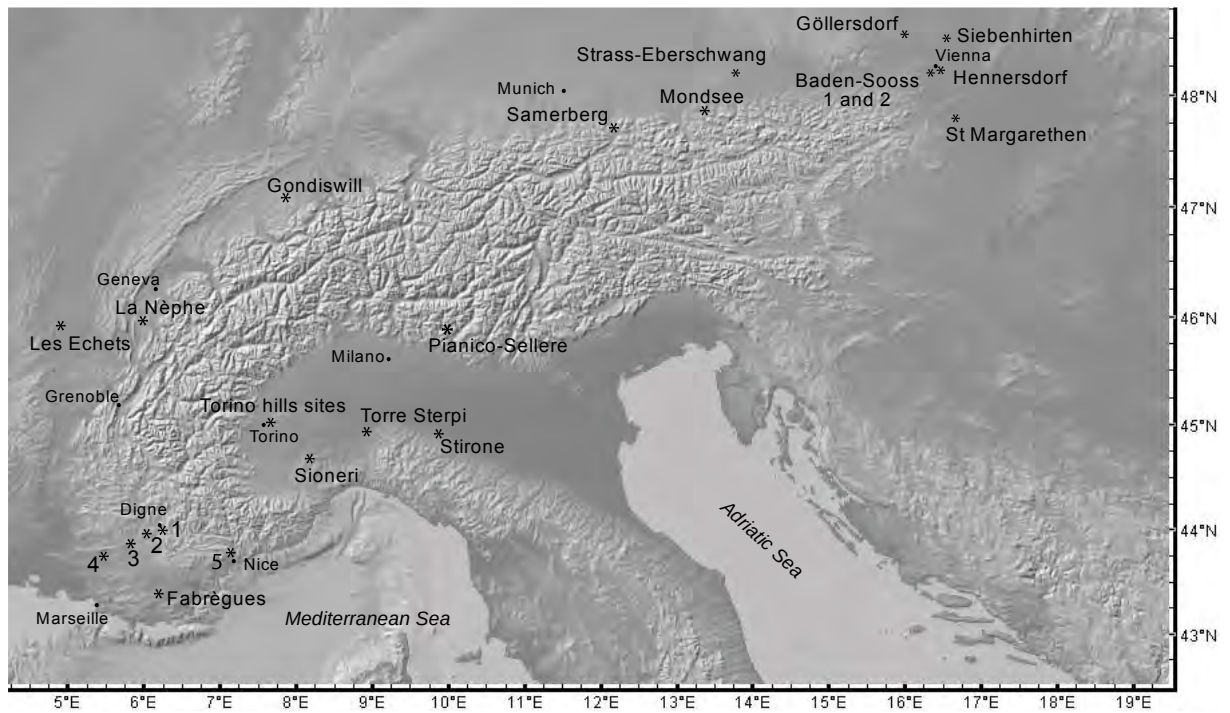


Fig. x.4. Location of the palynological sites mentioned in the text and in Figure x.3. The sites of the Torino Hills are: Gassinio Torinese, Tetti Civera (samples 1, 2 and 3) and Rio Civera, Pavarolo, Borelli. The numbered sites in Southern France are **1**) Saint Lions, Gambi, Châteauredon, Le Rochassas; **2**) La Rosée, Les Mées 1, Les Mées-Périgoite; **3**) Villeneuve, Oraison (Flour); **4**) La Motte d'Aigues, Vaugines; and **5**) Le Gour, Carros, Saint Martin du Var, Saint-Isidore.

On the whole, microtherm trees support the presence of boreal conditions (*Abies*, *Picea*) and meso-microtherm trees (particularly *Cathaya*) occur in significantly higher frequencies on the eastern side of the south-western Alps than on the western one (Figure x.4). This indicates that the present-day asymmetric topography of the south-western Alps, with a relatively gentle western flank and steeper eastern flank, was established early, and has been in existence since at least the early Miocene, and possibly since the Oligocene or late Eocene. Therefore, the high topography and asymmetric morphology of this part of the Alps has been maintained throughout the past ~30 Myrs.

In the East Eastern Alps, early to late Miocene pollen data (Figures x.3, x.4) show a very diverse flora (Jiménez-Moreno et al. 2005, 2008). The Burdigalian and Langhian (20.4–13.6 Ma) vegetation was dominated by thermophilous elements such as evergreen trees, typical of a present-day low altitude evergreen rain forest (e.g. south-eastern China), reflecting the MCO. During the Serravallian and Tortonian (13.6–7.2 Ma), important vegetation changes are observed: *Avicennia*, which previously populated the coastal areas up to these high latitudes, vanished and several other megatherm elements (*Buxus bahamensis*-type, *Alchornea*, Melastomataceae), typical of broad-leaved evergreen forests, became rarer before finally disappearing from Central Europe. These changes can be linked to cooling and correlated with global and regional climatic changes. Later, this vegetation was progressively replaced by communities rich in mesotherm plants. Percentages of mid- and high-altitude conifers increased considerably during the Langhian and later on during the Serravallian and Tortonian, indicating their relocation to a lower altitude, thus nearer to the sedimentation basin, which is correlated with significant cooling phases. These coniferous belts developed again at higher altitudes during warmer phases, as signalled by their reduced frequency in younger pollen records.

Subsequently, several thermophilous plants declined in abundance, and some of them disappeared from the Alps due to global cooling and progressive amplification of the glacial/interglacial cycles (see further details in Abels & Ziegler, this volume). The data from

the Stirone site (Figure x.3; Bertini 2001) at the foot of the Apennines, are a good example of this phenomenon. From their onset, glacial-interglacial cycles are marked by changes in both vegetation and reconstructed climate compared to the early Pliocene (Fauquette & Bertini 2003). During interglacials, the climate was almost as warm as in the early Pliocene, and the vegetation remained a mega-mesotherm to mesotherm plant forest. During glacials, mega-mesotherm taxa disappeared (e.g. *Distylium*, *Myrica*) or declined in abundance and in distribution (*Taxodium*-type, *Sequoia*-type). Temperatures were markedly lower than during interglacials—nearly equal to modern values—and not suitable for these thermophilous taxa.

The known macrofloras mostly come from the northern and eastern borders of the Alps for the Eocene to mid-Miocene interval (Mai 1995), and from the southern Alps for the Messinian and Pliocene (Bertini & Martinetto 2011; Martinetto et al. 2015). In general, these data confirm the picture provided by pollen with respect to the flora and vegetation of the lowland Alpine fringes. The most interesting information added by macrofossils is connected with the marked climatic cooling that has occurred since ~2.6 Ma: several plants now extinct in Europe entered the macrofossil record for the first time during this period (Martinetto et al. 2015). The cones of *Picea florschuetzii*, which are very similar to a modern spruce that grows in the Himalaya (*P. smithiana*), or *Tsuga chairugii*, whose relatives today live only in America and East Asia, are frequent in a few early Pleistocene sites of northern Italy (Ravazzi 2003). The presence of these taxa indicates either the descent of the Alpine high vegetation belts or immigration from Northern Europe/Siberia. Reliable records of plant species typical of the modern Alpine high altitude belt (e.g. *Larix* cf. *decidua* and *Picea abies*) are first found only in the late early Pleistocene (Ravazzi et al. 2005). Records of diagnostic species of the alpine belt are restricted to the late Pleistocene glacials and most commonly occur in the lowlands to the north of the Alps (e.g. *Salix herbacea*; Alsos et al. 2009). This appears to be a good example of a taphonomic window, where alpine taxa are only preserved when they descend close to potential depositional environments, which are restricted to lowlands or basin floors.

Very few pollen data are available from the Pleistocene. Pollen data from Pianico-Sellere (Bergamo, Italy; Figure x.4), attributed to early-middle Pleistocene, represent vegetation dynamics similar to those of the late Pleistocene interglacials but “Tertiary relicts” (*Pterocarya*, *Tsuga*, *Rhododendron ponticum*) are still present (Martinetto 2009). Other pollen successions in Switzerland and Bavaria attributed to the mid-Pleistocene (Welten 1982; Grüger 1983) illustrate, as elsewhere in Europe, a moderate expansion of *Pterocarya* during the Holstein interglacial. Several pollen records from France, Switzerland, Bavaria and Austria (respectively Les Echets, de Beaulieu & Reille 1984; Gondiswill, Wegmüller 1992; Samerberg, Grüger 1979; and Mondsee, Drescher-Schneider 2000; Figure x.4) document the vegetation dynamics of the last interglacial (Eemian), highlighting the significant role played by *Carpinus betulus* and the quasi-absence of *Fagus*.

x.3.2 The onset of modern vegetation: an example from the Western Alps

Numerous pollen records are available in the western Alps for the Holocene, which allow for the depiction of the general trend of vegetation changes during this period.

The Last Glacial Maximum between 24 and 17 ka (calibrated ages) constitutes the state of maximal retreat of temperate vegetation types, to the benefit of alpine-boreal plant communities. Temperate taxa were mostly restricted to southern refuges mainly located in the Iberian, Italian and Balkan peninsulas and around the Black Sea, but some of them could have also survived within cryptic northern refugia (e.g. Nieto Feliner 2011). Most of the temperate plant recolonisations occurring thereafter originated from southern regions (e.g. Brewer et al. 2002; Muller et al. 2007).

The Lateglacial period (17–11.3 ka) was marked by an ecological succession arising from an initial climate warming: the cold steppe vegetation dominated by *Artemisia* and *Amaranthaceae* was replaced by *Juniperus* scrub, then *Betula* woods and finally *Pinus* forests

(de Beaulieu & Reille 1983). The Younger Dryas climatic event, which allowed a widespread expansion of steppe communities throughout Europe, led to a general lowering of the tree line to ~300 m.

The subsequent temperature increase at the beginning of the Holocene induced a second phase of successional dynamics, involving temperate tree communities that replaced *Pinus* forests. The first trees to establish were *Corylus* and deciduous *Quercus*. They constituted, from sea-level to about 1800 m, diversified forests including *Fraxinus*, *Ulmus* and *Tilia*. At higher altitudes these forests were replaced by coniferous forests.

Simultaneously, around 10.1 ka, *Abies alba* penetrated into the southern French Alps, migrating from its nearest refugium in the northern Adriatic region (Muller et al. 2007). Fir forests expanded during the Atlantic period (8.9–5.4 ka), both in the southern (de Beaulieu & Reille 1983) and in the northern French Alps (David 1995). This range expansion was slower in the dryer internal massifs, and ended about 6.5 ka, when fir penetrated into the extensive pine woods of the most arid region of the Alps, the Briançonnais (Muller et al. 2007). Throughout its Alpine range, this highly competitive species found suitable conditions at middle altitudes, progressively forcing pines and *Larix decidua* to migrate to higher altitudes, and deciduous broad-leaved trees to migrate to lower altitudes.

Between 6.5 and 2.8 ka, *Pinus cembra* formed dense forests between 2000 and more than 2300 m (Muller et al. 2006). This occurred at the same time as an increase in the upper tree line, which exceeded 2900 m in the Queyras Valley (Talon et al. 1998). During the Subboreal period (5.4–2.8 ka), fir and deciduous oak declined as Neolithic human populations progressively colonized mountain territories (Walsh et al. 2014). The anthropogenic pressure was intense during the last 2.8 ka, since the beginning of the Subatlantic period, and the forest exploitation of the Bronze and Iron ages focused on some useful species, such as fir, which was intensively exploited to supply coastal shipyards (Nakagawa et al. 2000). Such human activity induced major vegetation changes from the shores to the mountains: at low altitudes, evergreen pioneer formations of *Quercus ilex* and *Pinus halepensis* replaced the deciduous forests of *Q. pubescens*, forming the anthropogenic meso-Mediterranean belt. At mid-altitudes, above the remnant deciduous oak forests of the supra-Mediterranean belt and within the mountain-Mediterranean belt, *Abies alba* forests declined to give way to *Fagus sylvatica*, while in the subalpine belt, *Pinus cembra* declined, and *Abies* disappeared from the internal valleys (Muller et al. 2007), which allowed larch and mountain pine to disperse to lower elevations.

During the Roman Empire, several cultivated trees were introduced (e.g. *Castanea*, *Juglans*) and the industrial forest exploitation (Nakagawa et al. 2000) allowed for the immigration of *Picea abies* into the newly opened vegetation zones. This species spread into the subalpine belt of the Northern Alps, where it found a suitably wet climate. The period between 500 and 1000 AD was marked by a forest recovery, then a new deforestation trend took place from the feudal times onwards, which finally ended during the Industrial Revolution of the 19th century. Thereafter, the abandonment of agriculture in remote valleys resulted in a re-establishment of mountain forests and the significant establishment of firs and oaks in secondary pioneer forests during the 20th century.

x.4 Climate and palaeoaltitude reconstructions of the Alps since the late Eocene

x.4.1 Methods based on pollen data

Pollen grains offer a large number of morphological traits (such as aperture, structure and sculpture) that can be analysed by light microscopy (Punt et al. 2007) and scanning electronic microscopy for surface features (Halbritter et al. 2007). These features can then be used to identify the pollen to species level. The implementation of these techniques in the 1970s led to

vastly improved identification rates of the Neogene pollen flora in the Mediterranean region, based on systematic comparative observations of fossil pollen grains with those of living plants (Suc 1976; Suc & Bessedik 1981). This botanical approach afforded the identification of more than 100 new taxa, including 14 robust identifications at the species level in the study area (*Avicennia officinalis*, *A. alba*, *Hamamelis mollis*, *Parrotia persica*, *Parrotiopsis jacquemontiana*, *Distylium chinense*, *Microtropis fallax*, *Juglans cathayensis*, *Nyssa sinensis*, *Rhoiptelea chiliantha*, *Carpinus orientalis*, *Rhus cotinus*, *Lygeum spartum*, *Cedrus atlantica*; Suc et al. 2004). This achievement significantly enriched the understanding of the regional Neogene flora and contributed to reliable climate reconstructions.

The climate reconstructions assembled from the Neogene data (Fauquette et al. 1999; Jimenez-Moreno et al. 2008; Fauquette et al. 2015) are based on the “climatic amplitude method,” which was developed by Fauquette et al. (1998) specifically to quantify the climate of periods with no modern analogues for the pollen spectra. In this method, the past climate is estimated by transposing the climatic requirements of the maximum number of modern taxa to the fossil data. This method takes into account pollen percentages and allows, despite some biases, for a greater refinement and precision of the climatic estimates because taxa with very low pollen percentages are not always significant. The most probable climate for a set of taxa is estimated as the climatic interval suitable for the highest number of taxa and a ‘most likely value’ corresponding to a weighted mean.

In this method *Pinus* pollen grains are excluded from the pollen sum as they are generally over-represented in marine sediments due to a prolific production and over-abundance due to long distance air and water transport (Heusser 1988; Beaudouin et al. 2007). High latitude/altitude taxa are also excluded from the reconstruction process to avoid a cold bias linked to pollen transport from higher elevations. The excluded taxa are defined on the basis of their occurrence in modern vegetation zones: vegetation types described for the studied time period are found today in south-eastern China. There, the vertical distribution of vegetation is characterized from the base to the top of the massifs by evergreen broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, *Picea/Tsuga* forest, *Abies* forest and high mountain meadows (Wang 1961; Hou 1983). This stratification allows us to exclude the modern high altitude taxa from the climatic reconstruction in order to infer the low to middle-low altitude climate (Fauquette et al. 1998). This procedure also allows us to discriminate between climatic variations and elevation changes.

Estimates based on this method showed that the latitudinal temperature gradient in western Europe was $\sim 0.48^{\circ}\text{C}/^{\circ}\text{latitude}$ during the mid-Miocene (Fauquette et al. 2007) and $\sim 0.46^{\circ}\text{C}/^{\circ}\text{latitude}$ during the early Oligocene (Fauquette et al. 2015) and that a modern gradient was established during the Tortonian.

The method to quantify palaeoaltitudes, developed by Fauquette et al. (1999), is based on pollen floras that provide a regional view of the vegetation from the lowest to the highest altitudinal belts feeding into the drainage basin from which the sediments were sourced and the mean annual temperature (MAT) reconstructed at sea level. The MAT is then transposed into a modern latitude. The latitude difference between the Cenozoic site and the modern latitude indicates the shift in altitude of the vegetation belts, in particular the *Abies/Picea* belt, which is the best indicator of elevated topography in the fossil pollen floras. The method uses a standard modern relationship established by Ozenda (1989, 2002), as the data do not allow the estimation of past terrestrial lapse rates. Ozenda’s relationship assumes that modern vegetation belts shift by 110 m in altitude per degree of latitude in the Alps. It should be noted that terrestrial lapse rates are highly variable geographically in relation to altitude, aspect of the slope, prevailing wind directions, continentality and atmospheric composition, among other factors and they are difficult to apply when the past atmospheric composition differed from the present (see chapter X, by Spicer). Meyer (1992) estimated modern terrestrial lapse rates for many areas of the world and found that they vary between 0.36 and $0.81^{\circ}\text{C}/100\text{ m}$ for MAT. However, because there is

no information concerning the palaeo-terrestrial lapse rates in the Alps, Fauquette et al. (2015) hypothesized that the ratio between altitudinal and latitudinal temperature gradients was similar to the present ratio. Taking into account the range of the modern terrestrial lapse rates, the relationship between the latitudinal and altitudinal gradients would vary and lead to different values for the shift of vegetation belts per degree in latitude (Table x.2). If this range of values is used the estimates of palaeoaltitudes would differ as well. However, Table x.2 highlights that the estimates of the terrestrial lapse rate for each studied period based on the standard modern relationship are included in Meyer's estimated range.

Table x.2. Shifts in altitude of the vegetation belts in relation to different terrestrial lapse rates and to the latitudinal gradients estimated for the different epochs (Fauquette et al. 2015). The minimum (0.36°C/100 m) and maximum (0.8°C/100 m) lapse rates are those reconstructed by Meyer (1992) for many areas of the world. The lines in bold corresponds to the estimates of the terrestrial lapse rate for each studied period based on the standard modern relationship.

	Latitudinal gradient (°C/° lat)	Terrestrial lapse rate (°C/100 m)	Shift in altitude/° in latitude
Standard modern	0.6	0.55	1° lat → 110 m altitude
Pliocene	0.6	0.36	1° lat → 167 m altitude
		0.55	1° lat → 110 m altitude
		0.81	1° lat → 74 m altitude
Middle Miocene	0.48	0.36	1° lat → 134 m altitude
		0.44	1° lat → 110 m altitude
		0.55	1° lat → 87 m altitude
		0.81	1° lat → 60 m altitude
Early Oligocene	0.46	0.36	1° lat → 128 m altitude
		0.42	1° lat → 110 m altitude
		0.55	1° lat → 84 m altitude
		0.81	1° lat → 57 m altitude

Moreover, palaeoelevation estimates correspond to the most probable palaeoelevations based on the 'most likely values' of MAT and to ranges of palaeoelevations based on the minimum and maximum MAT. This partially compensates for the use of the modern altitudinal/latitudinal ratio.

In the case of sites with unknown elevation (Suc & Fauquette 2012) that are all younger than 10 Ma in Fauquette et al. (2015), the latitudinal temperature gradient was similar to the modern one and the authors choose to keep the terrestrial lapse rate equivalent to the modern rate, taking into account that the position and continentality of the Alps was the same as today.

The record in the fossil pollen flora of microtherm trees such as *Abies* and *Picea* indicates elevated topography close to the sampled sites. Nevertheless, pollen data do not permit altitudinal range estimation for this vegetation belt, nor whether alpine herbaceous and perpetual-snow belts existed above it, due to difficulties in differentiating between the pollen of alpine herbaceous elements and those plants growing at lower elevations. As a consequence, these pollen-based palaeoelevations are minimum estimates corresponding to the lower limit of the highest forested belt.

We must emphasize the consistency of our previous estimates: the palaeoaltitude we inferred for the Mercantour Massif (Southwestern Alps) is consistent with a geomorphological reconstruction (Fauquette et al. 1999), the palaeoaltitude of the Ganos Mountain in the

Dardanelles Strait (Melinte-Dobrinescu et al. 2009) is in agreement with the tectonic hypothesis of Armijo et al. (1999) and the palaeoaltitude of the Canigou Mount in the Eastern Pyrenees (Suc & Fauquette 2012) is supported by a palaeogeographic validation (Clauzon et al. 2015).

x.4.2 Resulting palaeoaltitudes

Based on this method, the study by Fauquette et al. (2015) shows that the topography of the internal zone of the south-western Alps reached elevations of around 1800 m as early as the Oligocene (~30 Ma). In contrast, the external massifs, including the Mercantour Massif, uplifted later, during the late Neogene, while the post-Serravallian (~12–13 Ma) emplacement of the Digne thrust nappe was reinforced. Pollen data show that the present-day topographic asymmetry of the Southwestern Alps, with a relatively gentle western flank and much steeper eastern flank, dates back to at least the early Miocene, and possibly to the Oligocene or late Eocene.

In the East Eastern Alps (Jimenez-Moreno et al. 2008), palaeoaltitudes during the Burdigalian were not high enough for *Abies* and *Picea* to form forests, but sufficient to allow *Cathaya* to survive. Therefore, the relief was less than 1800 m. On the other hand, Serravallian and Tortonian pollen records, rich in conifers typical of high elevations, indicate an intense uplift during the mid-Miocene. The abundance increase in high elevation trees is due to uplift and not to climatic changes, as the pollen records are still dominated by thermophilous plants. Palaeoaltitudes were higher than 1600 m at that time.

x.5 How do regional geological evolution, global climatic changes and human pressure affect Alpine plant diversity and vegetation?

Due to the formation of the Alps since the late Paleogene (35–40 Ma) under warm-temperate to subtropical conditions, boreal-type environments could only develop at the higher elevations. Since the Oligocene, high elevations (~1800 m) allowed meso-microtherm (*Cedrus*, *Cathaya*) and microtherm (*Abies*, *Picea*) trees to establish.

The development of plant populations on mountains arises from two major sources (Ozenda 1985, 2009): an autochthonous (in situ) population formed of plants already present at the beginning of the uplift, and an allochthonous component arising from the migration from other cold regions.

The autochthonous part formed from a subtropical to tropical flora. Most of these taxa, vulnerable to cold, became extinct later due to glaciations and competition, but a few taxa such as *Juniperus thurifera* and *Berardia subacaulis* survived in the Western Alps (Ozenda 2009). Plants of temperate origin are represented by two groups: Holarctic and Mediterranean plants (Ozenda 1985).

The allochthonous part is made up of plants that migrated from the Mediterranean and/or central Asian mountains and Arctic regions (Ozenda 1995, 2009; Kadereit et al. 2008). Exchanges with Arctic and Northern European floras during glacials/interglacials is evidenced by the presence of “arctic-alpine” plants. However, the Alpine flora shows less pronounced affinities to the northern (Scandinavia, North America) than to the southern (Mediterranean Basin, Central and Eastern Asia) floras (Ozenda 1995, 2009; Comes & Kadereit 2003). The European Alpine system and major Central Asian mountains (Altai, Tibetan Plateau and Himalaya) are connected by a more or less continuous system of mountain ranges. This implies both a northern (boreal, subarctic, arctic) and a southern (southern mountains) connection between the European Alpine system and the Central Asian high mountains.

Pleistocene glaciations played a major role in the changing vegetation of the Alps: (1) the pre-existing thermophilous flora almost completely disappeared, (2) plants of temperate origin

only survived in refugia, leading to a disjunct distribution of some plants and (3) exchanges between the Alps and the other mountain ranges and/or northern regions were amplified. During glacial and interglacials warming phases led to the expansion of the thermophilous floras forcing microtherm plants to move towards colder areas to the north or to higher elevations (Ozenda 1985, 2009) resulting in disjunct distributions of arctic-alpine plants.

The postglacial period of the French Alps is the period in which the different vegetation belts recognized today were established (Table x.1). Around 10 ka, only two forested belts existed: a lower one, occupied by deciduous oak forest, and an upper one, characterized by coniferous forests (mainly *Pinus sylvestris* and *P. uncinata*). The boundary between these two belts was not abrupt, but formed a transition zone with mixed formations of oaks and pines. This intermediate belt only transformed into a belt in its own right with the immigration of fir, from ~9 ka. The fir forests, mixed with numerous deciduous trees, forced oak forests downslope and pine forests upslope. The late onset of this belt is clearly due to the migratory dynamics of fir that arrived in the French Alps from their Adriatic and Apennine refuges. Between 7.5 and 5 ka, the subalpine belt, which was made up of open woodlands of *Pinus uncinata* mixed with *Larix* and *Pinus cembra*, differed significantly from its modern physiognomy. The modern forest structure of this belt was only achieved around 5 ka with the development of dense forests of *P. cembra* up to ~2300 m. The onset of a real forested subalpine belt appears to be related to a general aridification, evidenced by low lake levels (Digerfeldt et al. 1997).

The last belt to appear in the Southwestern Alps was the lower meso-Mediterranean belt, at around 5–4 ka, characterized by the establishment of typical Mediterranean plants at low altitudes, in particular *Quercus ilex* and *Pinus halepensis*. The presence of Neolithic human populations supports the anthropogenic origin of this belt that corresponds to the replacement of deciduous forests by pioneer, disturbance-adapted plant formations. Nevertheless, recent multiproxy attempts to quantify Holocene climate fluctuations have shown that a succession of dry episodes from ~5 ka may have also triggered the expansion of sclerophyllous Mediterranean taxa (Magny et al. 2002). Unlike the other vegetation belts, the meso-Mediterranean belt appears to be a partly human-triggered subdivision of the former (supra-)Mediterranean belt, naturally dominated by deciduous oak forests. At higher altitudes, human activity also had strong effects, such as the lowering of the tree line by at least 300 m (Carnetti et al. 2004) and the creation of subalpine meadows. Moreover, increased human population size in mountains led to the fragmentation of forest ecosystems and thus to erosion events. In the second part of the 20th century, a policy of intensive reforestation started.

x.6 Conclusion

The flora of the Alps encompasses more than one-third of the European flora. Endemic taxa, mainly concentrated in the south-westernmost Alps and the south-western part of the Eastern Alps, represent 4% of the European flora. Maritime and Ligurian Alps constitute an important hotspot of plant species richness and form a major refugium where endemic plants represent 25% of all alpine endemics.

In the Alps, vegetation belts are organized by altitude, governed by decreases in temperature and increases in precipitation at higher elevations. These vegetation belts are well-recognized in modern pollen data established on two transects along the slopes of the Southwestern Alps. The modern pollen data also reflect the asymmetric west-east elevation of the massif: the replacement of pollen groups as elevation increases appears progressive on the western flank but much more abrupt on the eastern flank.

The formation of the Alps dates back to ~35 Ma and has influenced both the flora and the vegetation of the area, due to the appearance of high mountains, new marine basins and the consequent landscape fragmentation, environmental heterogeneities and new climatic patterns.

As early as the Oligocene, high relief allowed boreal-type environments to develop at the higher elevations and meso-microtherm (*Cedrus*, *Cathaya*) and microtherm trees (*Abies*, *Picea*) established early in the history of Alpine vegetation. During the Pleistocene, due to glaciations, the earlier, more thermophilous flora became extinct, while Arctic-alpine plants developed on the massifs. Holarctic plants only survived in refugia, leading to disjunct distributions. However, warm phases also led to disjunct distributions of the Arctic-alpine plants, which moved towards colder areas to the north or to higher elevations. Today only some “Tertiary relicts”, such as *Juniperus thurifera*, *Berardia subacaulis*, still survive in the Alps.

The onset of the modern vegetation patterns started in the early postglacial period, around 10 ka. The different vegetation belts recognized today gradually developed following local climate and soil conditions, and the migratory dynamics of the species. The presence of human populations in the Alps since the Neolithic triggered the expansion of some vegetation types, in particular typical Mediterranean plant formations at low altitude, and the lowering of the tree line that led to the development of the subalpine meadows. Finally, the recent abandonment of land cultivation has resulted in the return of mountain forests.

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Vegetation, climate and palaeoaltitude reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria, Central Europe

Gonzalo Jiménez-Moreno^{1,2*}, Séverine Fauquette³ and Jean-Pierre Suc¹

¹UMR 5125 PEPS, Université Lyon 1, Campus de La Doua, Bâtiment Géode, Villeurbanne Cedex, France, ²Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain, ³Institut des Sciences de l'Evolution CC 061, CNRS, Université de Montpellier 2, Place Eugène Bataillon, Montpellier Cedex, France

ABSTRACT

Aim To reconstruct the flora, vegetation, climate and palaeoaltitude during the Miocene (23.03–5.33 Ma) in Central Europe.

Location Six outcrop sections located in different basins of the Central Paratethys in Austria.

Methods Pollen analysis was used for the reconstruction of the vegetation and climate. The altitude of the Eastern Alps that are adjacent to the Alpine Foreland and Vienna basins has been estimated using a new quantification method based on pollen data. This method uses biogeographical and climatological criteria such as the composition of the modern vegetation belts in the European mountains and Miocene annual temperature estimates obtained from fossil pollen data.

Results Pollen changes from Early to Late Miocene have been observed. The vegetation during the Burdigalian and Langhian (20.43–13.65 Ma) was dominated by thermophilous elements such as evergreen trees, typical of a present-day evergreen rain forest at low altitudes (i.e. south-eastern China). During the Serravallian and Tortonian (13.65–7.25 Ma) several thermophilous elements strongly decreased, and some disappeared from the Central European region. This kind of vegetation was progressively substituted by one enriched in deciduous and mesothermic plants. Middle-altitude (*Cathaya*, *Cedrus* and *Tsuga*) and high-altitude (*Abies* and *Picea*) conifers increased considerably during the Langhian and later on during the Serravallian and Tortonian.

Main conclusions Pollen changes are related to climatic changes and to the uplift of the Alpine massifs. The vegetation during the Burdigalian and Langhian reflects the Miocene climatic optimum. The decrease in thermophilous plants during the Serravallian and Tortonian can be interpreted as a climatic cooling and can be correlated with global and regional climatic changes. This study shows that the palaeoaltitude of the eastern part of the Eastern Alps during the Burdigalian was not high enough for *Abies* and *Picea* to form a forest. Therefore, we inferred that the summits of most of the mountains would have been less than 1800 m. The substantial increase of middle- and high-altitude conifers in the pollen spectra suggests that the uplift rate increased during the Langhian in this region. Based on higher palaeoaltitude estimations for the pollen floras from the studied sections of Austria, we infer that the uplift of the easternmost part of the Alpine chain continued during the Serravallian and Tortonian.

Keywords

Altitude, Austria, climate, Eastern Alps, Miocene, palynology, tectonic uplift, vegetation reconstruction.

*Correspondence: Gonzalo Jiménez-Moreno, Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuente Nueva S/N, 18002 Granada, Spain.
E-mail: gonzaloj@ugr.es

INTRODUCTION

Pollen analysis has been proven to be a very efficient tool for reconstructing vegetation and climate for the Miocene in the Central Paratethys (Ivanov *et al.*, 2002; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005).

Reconstruction of palaeoaltitudes is fundamental to improving our knowledge of European palaeogeography during the Miocene. However, palaeogeographical reconstructions of palaeoaltitudes of Alpine massifs during the Neogene are scarce. They are based primarily on the sedimentary record, the flux of terrigenous sediments accumulated in sedimentary basins and facies distribution (Schmid *et al.*, 1996; Frisch *et al.*, 1998; Kuhlemann & Kempf, 2002; Braga *et al.*, 2003; Martín *et al.*, 2003; Kuhlemann, 2007) and thermochronology (i.e. fission track measurements: Hejl, 1997; Dunkl *et al.*, 1998; Bigot-Cormier *et al.*, 2000; Bistacchi & Massironi, 2000; Spiegel *et al.*, 2001; Herwegh & Pfiffner, 2005; Kuhlemann *et al.*, 2006; Zattin *et al.*, 2006).

A new method of quantification of palaeoaltitudes has been developed (Fauquette *et al.*, 1999) and is applied here to estimate palaeoaltitudes of the eastern part of the Eastern Alps during the Miocene. This method takes into account pollen floras accumulated near the coastline, providing both a regional view of the vegetation from the littoral to the uppermost altitudinal belts and climatic reconstructions. This new method improves upon previous work using macrofloras to estimate past altitudes (Axelrod, 1965, 1968; Axelrod & Bailey, 1976; Meyer, 1992). These previous studies were based on macroremains that provided a fragmentary and very circumscribed idea of the vegetation. They were located at mid to high altitudes in north-western America and have no direct link to the altitudinal climatic gradient from sea level. This method has been successfully applied to Early Pliocene pollen spectra from the Mercantour Massif in the Southern Alps (Fauquette *et al.*, 1999) and the Canigou Mountain in the eastern Pyrenees (Pérez Villa *et al.*, 2001). In both studies the results were validated by geomorphology (Fauquette *et al.*, 1999; Clauzon *et al.*, 2002).

The aims of this study are to reconstruct the vegetation developed around the Alpine Foreland and Vienna basins (Austria) during the Miocene and give an interpretation in terms of climate and palaeoaltitudes. Our analyses are based on pollen analysis of several sections distributed throughout the Miocene using botanical taxonomy and a quantitative analysis of the pollen data.

PALAEOGEOGRAPHICAL FRAMEWORK

Palaeogeographical changes influence climate and floral and faunal exchanges. Tectonic processes were very active during the studied time period and played a major role by causing important palaeogeographical changes, which produced modifications in oceanic/atmospheric circulation (such as the marine gateway openings of the Denmark Strait and Drake

Passage and the closure of the seaway between the Mediterranean Sea and the Indian Ocean) that generated the Miocene climatic cooling (Pagani *et al.*, 2000; Billups *et al.*, 2002; Ogasawara, 2002; Diekmann *et al.*, 2003; Hall *et al.*, 2003; Meulenkamp & Sissingh, 2003).

Alpine uplift started 35 million years ago (Ma), during the Eocene–Oligocene transition (Meulenkamp & Sissingh, 2003; Jolivet *et al.*, 2006; Popov *et al.*, 2006), principally due to two contemporary processes: (1) migration of the African plate northward, then collision with the European plate producing subduction of the European plate below Apulia; and (2) slab retreat and coeval back-arc basin opening (Jolivet *et al.*, 2006; and references therein). The subduction and ensuing collision processes led to the formation of mountain belts from the Betic Cordillera and the Rif in the west, to the Hellenides and Taurides in the east. The formation of the Alps and Carpathians was due to the subduction of the European plate below Apulia, part of the African plate. The retreat of the European slab allowed the formation of the Pannonian Basin to the east, although its dynamics cannot be compared simply to the true back-arc basins of the Mediterranean region (Linzer, 1996; Horvath & Tari, 1999; Wortel & Spakman, 2000; Cloething *et al.*, 2004). The convergence between the African and Eurasian plates led to the Tethys becoming a geo- and biogeographical palaeoentity and the development of two distinct physiographical realms during the Miocene and Pliocene (23.03–1.81 Ma): the Mediterranean and Paratethys seas (Rögl, 1998; Meulenkamp & Sissingh, 2003). Because of this convergence, numerous marine and continental basins were generated on the northern Mediterranean margin and on the Paratethys. During the Miocene and Pliocene, these basins experienced a long-term trend of decreasing marine influence and concomitant reduction in the size of their marine depositional domains (Rögl, 1998; Meulenkamp & Sissingh, 2003; Popov *et al.*, 2006). Furthermore, also due to this convergence, the Eurasian plate drifted northward (Meulenkamp & Sissingh, 2003). Several palaeomagnetic studies estimate a drifting value of *c.* 10° since the Early Miocene until the Present. Average values for the studied span [Early Burdigalian (20 Ma)–Late Tortonian (8–7 Ma)] are *c.* 3°–4° (Rögl, 1998; Meulenkamp & Sissingh, 2003). This would have contributed to the general climate cooling on these moving continental masses during the Miocene and thus has to be taken into account.

MATERIALS AND METHODS

Studied sections

In this study, 48 samples from six outcrop sections, previously well dated by different methods, were analysed for pollen grains. Samples came from different basins of the Central Paratethys in Austria (Fig. 1). The sections studied from Burdigalian to Tortonian are (from west to east): Strass-Eberschwang [Alpine Foreland Basin, Ottnangian (Burdigalian) *c.* 18 Ma; Faupl & Roetzel, 1987]; Göllersdorf [Alpine

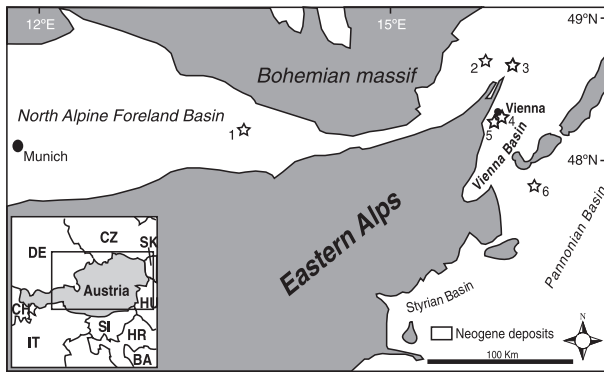


Figure 1 Geographical map with the location of the studied sections (white stars): (1) Strass-Eberschwang; (2) Göllersdorf; (3) Siebenhirten; (4) Hennersdorf; (5) Baden-Sooss 1 and 2; and (6) St Margarethen. Modified from Jiménez-Moreno (2005).

Foreland Basin, Karpatian (Upper Burdigalian), *c.* 16.5 Ma; Roetzel *et al.*, 1999]; Baden-Sooss-1 [Vienna Basin, Lower Badenian (Langhian), *c.* 14.5 Ma; Fuchs & Stradner, 1977]; Siebenhirten [Vienna Basin, Lower Sarmatian (Upper Serravallian), *c.* 12.4 Ma; Harzhauser & Piller, 2004a]; Baden-Sooss-2 [Vienna Basin, Upper Sarmatian (uppermost Serravallian), *c.* 12 Ma; Brix, 1988]; St Margarethen [Eisenstadt-Sopron Basin, Upper Sarmatian (uppermost Serravallian), *c.* 11.8 Ma; Harzhauser & Kowalke, 2001; Harzhauser & Piller, 2004b]; and Hennersdorf [Vienna Basin, Pannonian (Tortonian), *c.* 10.3 Ma; Magyar *et al.*, 1999; Harzhauser & Mandic, 2004].

Pollen analysis

Sampling was done by taking *c.* 150 g of sediment per sample. In the chemical treatment, only 15–20 g of sediment were used. The samples were processed with cold HCl (35%) and HF (70%), removing carbonates and silica. Separation of the palynomorphs from the remaining residue was carried out using ZnCl₂ (density = 2). Sieving was done using a 10-µm nylon sieve. The pollen residue, together with glycerin, was prepared on slides. A transmitted light microscope, using ×250 and ×1000 (oil immersion) magnifications, was used for botanical identification and counting of palynomorphs, palynomorphs being very abundant in these sediments. Spores were not considered due to their low abundance.

Identification of the pollen grains was done by comparing the Miocene grains with their present-day relatives using the pollen and photograph collections stored in the laboratory in Lyon, several pollen atlases (China, Taiwan, Africa, North America, Mediterranean region, etc.) and the Photopal website (<http://medias.obs-mip.fr/photopal>). A minimum of 150 terrestrial pollen grains, *Pinus* and indeterminate Pinaceae excluded, were counted in each sample.

Detailed pollen diagrams and standard synthetic diagrams (Suc, 1984), without *Pinus* and indeterminate Pinaceae, have been plotted (Figs 2–4). In Fig. 4, taxa have been grouped into 10 different groups based on ecological criteria (Nix, 1982) in

order to clearly visualize the composition of the past vegetation (see Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005, for an explanation of the grouping). Complete pollen data will be made available on the web in the 'Cenozoic Pollen and Climatic values' database (CPC) (<http://cpc.mediasfrance.org>).

Climate reconstruction

Climate reconstructions, based on pollen data, were estimated using the climatic amplitude method (Fauquette *et al.*, 1998a,b). This method has been applied to many pollen sequences of the western Mediterranean area (Fauquette *et al.*, 1998a, 1999; Fauquette & Bertini, 2003; Jiménez-Moreno *et al.*, 2005, 2007; Fauquette *et al.*, 2006) and has also been applied to the pollen sequences presented herein. This will allow us to estimate the climate in Austria throughout the Miocene period. The climatic amplitude method is a method in which the past climate is estimated by transposing the climatic requirements of the maximum possible number of modern taxa to the fossil data. The most probable climate for a set of taxa is estimated as the climatic interval suitable for the highest number of taxa. High-latitude/high-altitude taxa were excluded from the reconstruction process. The identification and exclusion of high-latitude/high-altitude plants is based on numerous palynological studies (Suc *et al.*, 1995a,b, 1999; Jiménez-Moreno, 2005) that show that the Neogene vegetation zonation followed a similar latitudinal and altitudinal zonation to the one observed in present-day south-eastern China (Wang, 1961), where most of the taxa that disappeared from Europe by the Late Neogene can be found. Therefore, the estimates obtained correspond to the climate at low to middle–low altitude (Fauquette *et al.*, 1998a). The pollen grains of *Pinus* and indeterminate Pinaceae have been excluded from the pollen sum as they are, in some cases, over-represented.

The results are presented, as potential climate ranges and a 'most likely value' corresponding to a weighted mean, for two climatic parameters: (1) mean annual temperature (Ta); and (2) mean annual precipitation (Pa).

Palaeoaltitude reconstruction

Altitudinal zonation of plants reflects their latitudinal distribution. For example, today, the *Abies–Picea* vegetation belt ranges between 0 and 500 m a.s.l. in altitude in southern Sweden and southern Norway (Noirfalise *et al.*, 1987), but it is situated between 1400 and 2000 m in the southern French Alps (Ozenda, 1961) (Fig. 5). The vertical shift of the vegetation belts in relation to latitude is obvious but difficult to quantify, as the elevational range of plant species is controlled not only by climatic parameters (decreasing temperature and increasing precipitation with increasing altitude), but also by local conditions (nature of soils, slope orientation, etc.). Ozenda (1975) attempted to quantify the vertical shift in relation to latitude in Europe based on three

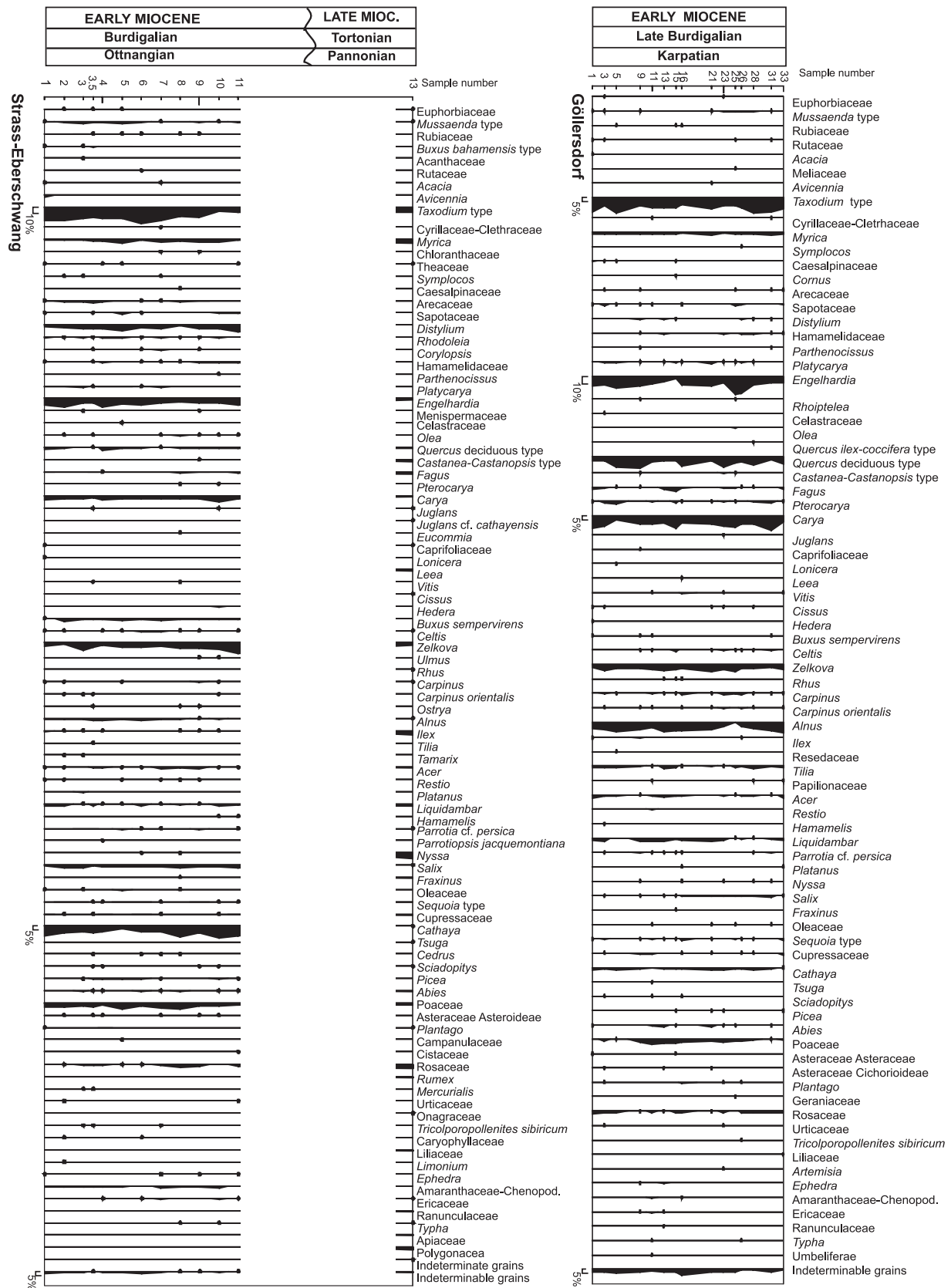


Figure 2 Detailed pollen diagrams showing percentages of taxa of the Strass-Eberschwang and Göllersdorf sections without *Pinus* and indeterminate Pinaceae. A solid dot indicates taxa recorded in the counts but at percentages below 1%.

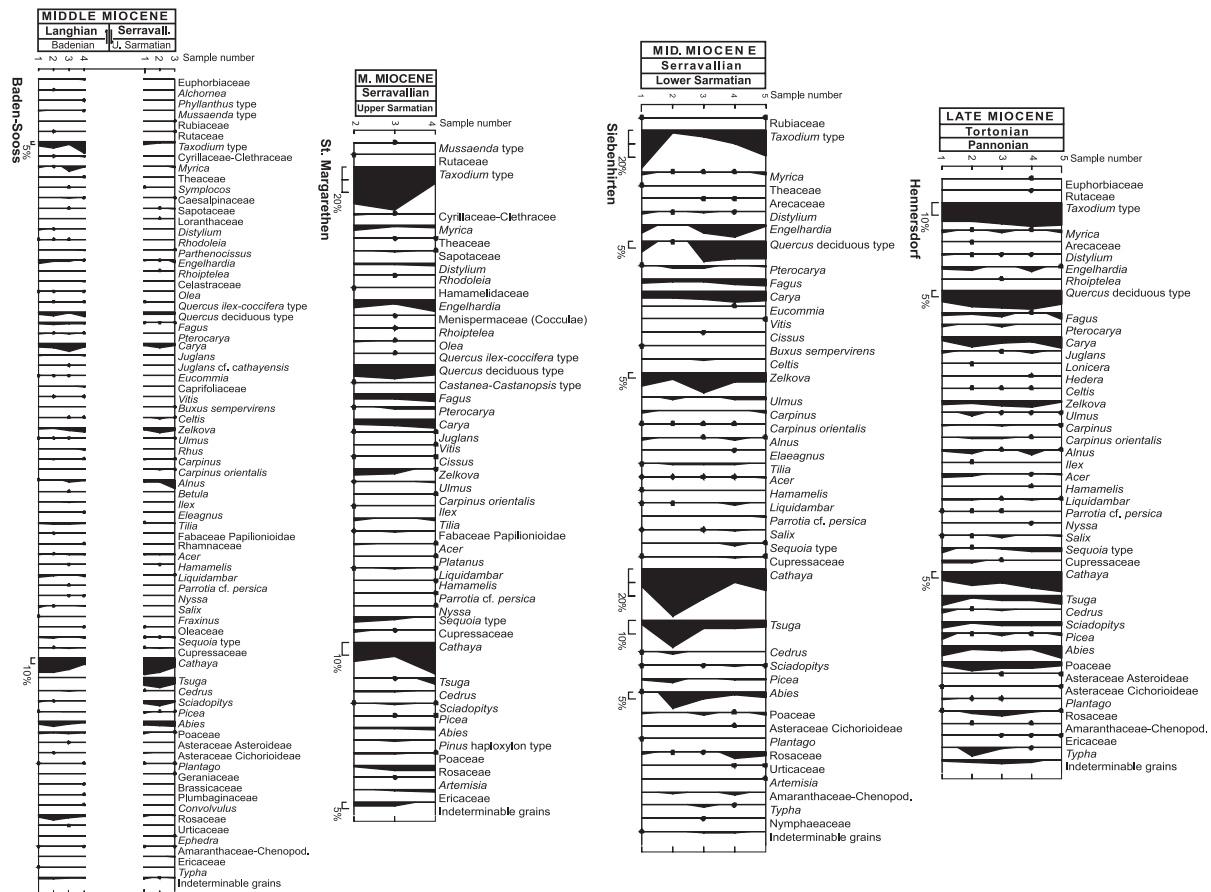


Figure 3 Detailed pollen diagrams showing percentages of taxa of the Baden-Sooss 1 (lower portion) and 2 (upper portion), St Margarethen, Siebenhirten and Hennersdorf sections without *Pinus* and indeterminate Pinaceae. A solid dot indicates taxa recorded in the counts but at percentages below 1%.

observations: (1) vegetation belts occur at different altitudes at different latitudes; (2) in temperate regions, mean annual temperatures vary *c.* 0.6°C per degree in latitude (1° in latitude = *c.* 110 km); and (3) temperature decreases in relation to altitude at *c.* 0.55°C per 100 m of elevation. Ozenda (1989) established the following relationship: a shift of 1 km to the north is equivalent, from a bioclimatic point of view, to a shift of 1 m in altitude. As a result, today, in general, vegetation belts shift 110 m in altitude per degree in latitude. Using this relationship, the vegetation distribution during the Miocene and the pollen-based climate estimates, it is possible to estimate the altitude of the Eastern Alps throughout the Miocene. In this study, conifers from high-elevation vegetation belts (mainly *Abies* and *Picea*) are used as the best indicators of palaeoaltitude in the pollen spectra. Based on modern pollen spectra from marine sediments close to the Alps (Suc *et al.*, 1999), a threshold value of 3% for *Abies* and *Picea* has been used to infer the presence of *Abies* and *Picea* forests in the past. In order to estimate palaeoaltitudes, the following assumptions have been made: (1) the present climatic limits of the closest living taxa are the same as those of the Miocene plants; (2) the pole-to-equator

climatic gradient was similar to that of today, and hence the poleward lowering of the elevational limits of plant species or zones would be similar to that of today; and (3) the elevational zonation of plants during the Miocene in Central Europe was similar to the present-day zonation in south-eastern China.

RESULTS

Vegetation belts

A very rich and diverse flora has been recorded in this study (Figs 2 & 3). The vegetation has been compared with the one growing today in subtropical to temperate south-eastern China (Wang, 1961), the most reliable present-day model (Suc, 1984; Axelrod *et al.*, 1996; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005). The following plant ecosystems can be distinguished in the pollen data:

(1) A coastal marine environment characterized by the presence of an impoverished mangrove composed of *Avicennia*, which is mainly accompanied by halophytes (such as *Amaranthaceae*–*Chenopodiaceae* and *Armeria*).

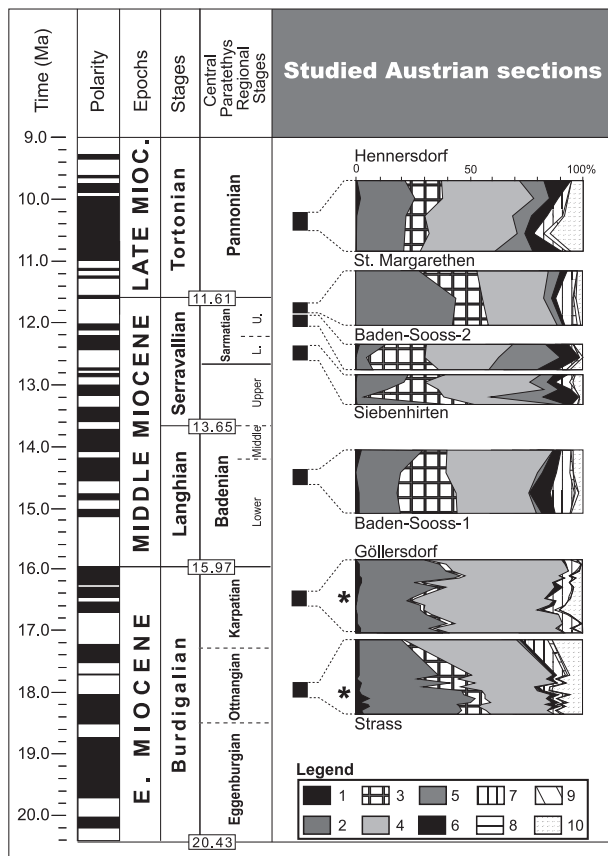


Figure 4 Chronostratigraphical situation (according to the time-scale of Harzhauser & Piller, 2007) and pollen synthetic diagrams without *Pinus* and indeterminable Pinaceae of the studied sections from Austria. The stratigraphical lengths of the sections are approximate (see references in the text for more details). Grouping was done regarding the ecology of the plants (see text for explanation). Legend numbers are: (1) megathermic elements (i.e. tropical); (2) mega-mesothermic elements (i.e. subtropical); (3) *Cathaya*; (4) mesothermic elements (i.e. warm-temperate); (5) meso-microthermic elements (mid-altitude conifers); (6) microthermic elements (high-altitude conifers, mainly *Abies* and *Picea*); (7) non-significant elements; (8) Cupressaceae; (9) Mediterranean xerophytes; (10) herbs and shrubs. The asterisk indicates the presence of pollen of *Avicennia* (mangrove plant).

(2) A broad-leaved evergreen forest, from sea level to around 700 m in altitude, featuring *Taxodium* or *Glyptostrobus*, *Myrica*, *Rhus*, Cyrillaceae–Clethraceae, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Hedera*, Hamamelidaceae, *Engelhardia* and *Rhoiptelea*.

(3) An evergreen and deciduous mixed forest above 700 m in altitude, characterized by deciduous *Quercus*, *Engelhardia*, *Platycarya*, *Carya*, *Pterocarya*, *Fagus*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis* and *Acer*. Within this vegetation belt, a riparian vegetation has been identified, composed of *Salix*, *Alnus*, *Carya*, *Carpinus*, *Zelkova*, *Ulmus* and *Liquidambar*. The shrub layer was dominated by Ericaceae, *Ilex* and Caprifoliaceae.

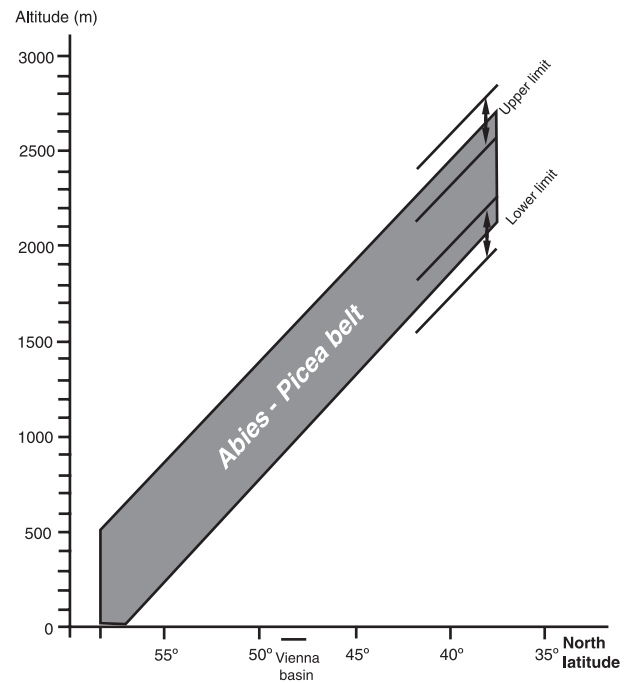


Figure 5 Altitudinal variation of the *Abies*–*Picea* belt in relation to latitude, from north to south, and the present latitudinal position of the Vienna Basin.

(4) From 1000 m up, a mid-altitude deciduous and coniferous mixed forest with *Betula*, *Fagus*, *Cathaya*, *Cedrus* and *Tsuga*.

(5) Lastly, above 1800 m in altitude, a coniferous forest with *Abies* and *Picea*.

Vegetation dynamics

Burdigalian–Langhian (Ottangian to Middle Badenian)

Pollen spectra from Strass-Eberschwang, Göllersdorf and Baden-Sooss-1 demonstrate the regular occurrence and abundance of thermophilous species typical of the lowest altitudinal belts described above and the relative scarcity of altitudinal elements (Figs 2 & 3).

The coastal marine environment was generally composed of the *Avicennia* mangrove (its presence during the Burdigalian in Strass-Eberschwang and Göllersdorf and during the Langhian in other sections from Central Europe was recorded in Nagy, 1990; Nagy & Kókay, 1991; and Plaziat *et al.*, 2001) and several halophytes.

In the hinterland, the lowlands were populated by a broad-leaved evergreen forest, depicted by *Alchornea*, *Rhus*, Theaceae, Rubiaceae, Chloranthaceae, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Hedera*, Hamamelidaceae, *Engelhardia*, *Rhoiptelea*, etc. Within this vegetation belt, the swamp forests were also well developed during this time period. Its components, such as *Taxodium* or *Glyptostrobus*, *Nyssa*, *Myrica* and Cyrillaceae–Clethraceae, show comparatively high abundances in the pollen spectra. Very humid

conditions at that time most likely favoured the wide distribution of swamp forests and of ecologically related riparian forests with *Platanus*, *Liquidambar*, *Zelkova*, *Carya*, *Pterocarya* and *Salix*.

An evergreen and deciduous mixed forest composed mainly of elements such as *Quercus*, *Carya*, *Pterocarya*, *Fagus*, *Ericaceae*, *Ilex*, *Caprifoliaceae*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis* and *Acer*, but also *Engelhardia* and *Platycarya*, characterized areas of higher altitude. Within this vegetation belt, a riparian vegetation has been identified, mainly composed of *Salix*, *Alnus*, *Carya*, *Carpinus*, *Zelkova* and *Ulmus*.

Mid- and high-altitude elements (*Tsuga*, *Cedrus*, *Abies* and *Picea*) and *Cathaya* increased significantly during the Langhian (Baden-Sooss-1 section; Figs 3 & 4).

Serravallian–Tortonian (c. Late Badenian to Pannonian)

Important changes in the vegetation are observed in Siebenhirten, Baden-Sooss-2, St Margarethen and Hennesdorf sections: *Avicennia*, which previously populated the coastal areas, vanished and several megathermic elements (*Buxus bahamensis* group, *Alchornea* and *Melastomataceae*), typical of the broad-leaved evergreen forest, became rare and most of them disappeared from the region (Figs 3 & 4). This is in accordance with previous studies that also show the disappearance of *Avicennia* and several megathermic plants from Central Europe during the same time-span (Plaziat *et al.*, 2001; Jiménez-Moreno, 2005).

The evergreen–deciduous mixed forest suffered a great transformation due to the loss and decrease in the abundance of several mega-mesothermic evergreen plants. Deciduous mesothermic plants, such as deciduous *Quercus*, and *Fagus*, *Alnus*, *Acer*, *Eucommia*, *Betula*, *Alnus*, *Carpinus*, *Ulmus*, *Zelkova* and *Tilia*, progressively substituted this kind of

vegetation. Thus, the vegetation shows a tendency towards increasing proportions of mesothermic deciduous elements, which most likely came from higher altitudes. However, the swamp forest continued to be very well developed.

At the same time, the vegetation from mid-altitude (*Cathaya*, *Tsuga* and *Cedrus*) and high-altitude (*Picea* and *Abies*) belts clearly increased (Fig. 4). A similar vegetation change is observed during the same time interval in other areas of Europe (e.g. Spain, southern France, Switzerland and Hungary: (Bessedik, 1985; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005).

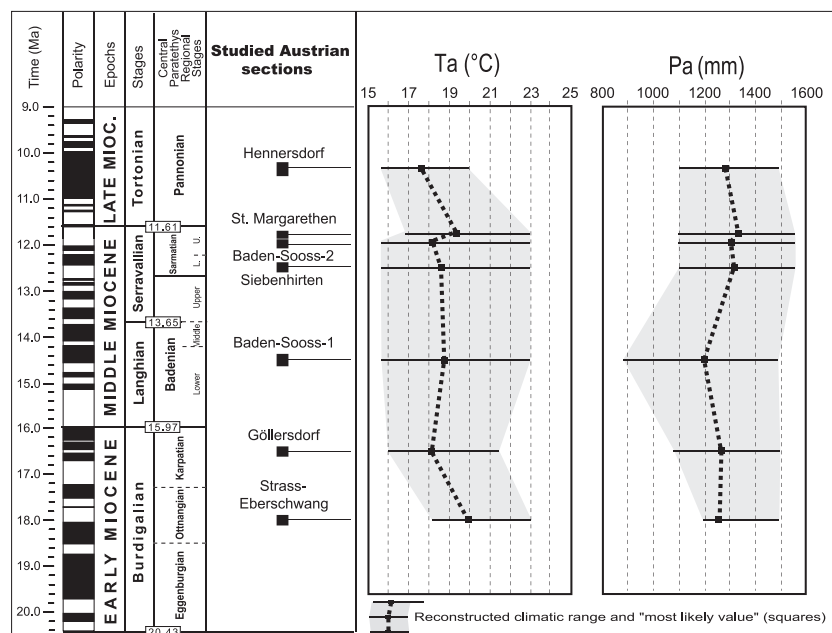
Palaeoaltitude estimation

Burdigalian–Langhian

During the middle Burdigalian (c. 18 Ma), the estimated mean annual temperature on the coastline at Strass-Eberschwang was c. 20°C (Fig. 6). Therefore, the *Abies* and *Picea* belt would have developed at a high altitude in order to compensate for the high temperatures. Today, such a temperature occurs in south-eastern China where *Abies* is present above an altitude of 1800 m (Wang, 1961). Pollen percentages in samples from the Strass-Eberschwang locality show a maximum value of 1.3% of the high-altitude elements *Abies* and *Picea* (Fig. 4). These elements are not abundant in the pollen spectra, indicating altitudes < 1800 m. On the contrary, *Cathaya*, growing today between 900 and 1900 m in south-eastern China (Liu *et al.*, 1997), is quite abundant in the samples. Therefore, we can infer a maximum elevation between 900 and 1800 m for the eastern part of the Eastern Alps at c. 18 Ma.

Later, during the late Burdigalian (c. 16.5 Ma) at Göllersdorf, the maximum values of *Abies* and *Picea* were 2.15%

Figure 6 Chronostratigraphical situation (according to the time-scale of Harzhauser & Piller, 2007) and climatic reconstruction based on the pollen data (mean annual temperature and mean annual precipitation) from the studied sections. The stratigraphical lengths of the sections are approximate (see references in the text for more details). Only the average temperature (Ta, °C) and precipitation (Pa, mm) for all the pollen samples in each section has been plotted.



(Fig. 4). Therefore, as in Strass-Eberschwang, palaeoaltitudes would be < 1800 m.

In the samples from Baden-Sooss-1 of Langhian age (c. 14.5 Ma), the maximum value of *Abies* and *Picea* of 3.98% (Fig. 4) indicates that this vegetation belt was well developed in the mountains close to Baden-Sooss. The estimated mean annual temperature was around 18.8°C (range between 15.6°C and 22.9°C). Today, such a temperature occurs at c. 36° latitude (e.g. in Malta), c. 12° lower in latitude than Baden-Sooss. However, we have to take into account that during the Langhian, Europe was located around 3° lower in latitude than today (Meulenkamp & Sissingh, 2003). Therefore, after this subtraction (12°–3°), we can estimate a latitude of c. 9° lower for the above estimated temperature. Using the ratio established by Ozenda (1989), a shift of 9° in latitude would correspond to a shift of c. 990 m in altitude. Today, the lower altitudinal limit of *Abies* in the closest mountains is situated around 600 m (Ozenda *et al.*, 1979). Taking into account the shift of 990 m in vegetation belts between the Langhian and present day, *Abies* would be present above 1590 m. This indicates that, during the Langhian, the eastern part of the Eastern Alps was at least 1600 m above sea-level.

Serravallian–Tortonian

Pollen spectra younger than the Langhian (Siebenhirten, Baden-Sooss-2, St Margarethen and Hennersdorf; c. 12.4, 12, 11.8 and 10.3 Ma, respectively) show high percentages of *Abies* and *Picea* (Fig. 4). This implies that since the Langhian, this vegetation belt would have been fully developed and we are no longer able to estimate palaeoaltitudes. Therefore, the Eastern Alps were at least 1600 m high.

DISCUSSION

Climatic evolution

The large number of thermophilous elements during the Early and early Middle Miocene suggests a warm, subtropical climate. The climate was also quite humid, which was necessary to support the development of such a large association of thermic elements, which require very humid conditions all year (Wang, 1961). The estimated climatic parameters indicate mean annual temperatures of around 18–20°C and mean annual precipitations between 1200 and 1300 mm (Fig. 6). The floral assemblages and climatic parameters during the Early and early Middle Miocene clearly reflect the Miocene Climatic Optimum (MCO: Zachos *et al.*, 2001; Shevenell *et al.*, 2004). These results are in accordance with other palaeobotanical data from Central Europe that also indicate very warm floras and high temperature estimations for the Early and early Middle Miocene. For example, Jiménez-Moreno *et al.* (2005) show, from estimates based on Karpatian and Early Badenian (Langhian) pollen floras from Hungary, a good correspondence not only in temperature [mean annual temperature (MAT) = 18–20°C], but also in precipitation [mean annual precipitation

(MAP) = 1200–1400 mm]. Mosbrugger *et al.* (2005), using abundant palaeobotanical data from Germany, noticed increases in all of the temperature records in three Cenozoic basins during the mid-MCO. Böhme *et al.* (2007), studying xylofloras from the North Alpine Foreland Basin (in southern Germany), also showed very high temperature estimations of c. 22.2–24.2°C (MAT) during the Late Ottnangian (Early Miocene) and 17.4–20.5°C (MAT) for the early Middle Miocene. A mean annual temperature of around 18°C was estimated using macrofloras for the mid-Miocene climate optimum in Serbia (Utescher *et al.*, 2007). Erdei *et al.* (2007) also calculated high temperatures of c. 18.8–16.5°C (MAT) for the Early Miocene using macrofloras from the Pannonian Basin.

The major change in the pollen spectra is the observed impoverishment in plant diversity produced by the disappearance of some of the most thermophilous plants and the consequent enrichment in mesothermic and altitudinal plants, from the Serravallian up to the Tortonian. Palaeoclimatic parameter estimates show the lowest MAT values in Hennersdorf (Tortonian) of c. 17–18°C (Fig. 6). Despite a general decreasing trend in our temperature estimates during the Middle and Late Miocene (Fig. 6), there is also a positive excursion during the Late Sarmatian (St Margarethen section; Fig. 6). This warm peak during the Late Sarmatian has also been observed by Piller & Harzhauser (2005) and Harzhauser *et al.* (2007) (who report positive $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values and a low sea level) and could be related to orbital climate forcing (see Jiménez-Moreno *et al.*, 2005, for explanation). This is related to a gradual decrease in temperatures immediately following the MCO, which has also been observed in several palaeobotanical studies in Central Europe, with decreases in temperature of c. 1.5°C in the Forecarpathian Basin (Ivanov *et al.*, 2002), 2–3°C in Hungary (Jiménez-Moreno *et al.*, 2005), c. 2°C in the Pannonian Basin (Erdei *et al.*, 2007) and 2–3°C in Serbia (Utescher *et al.*, 2007) and Germany (Mosbrugger *et al.*, 2005). This gradual temperature decrease is well documented on a world-wide scale and has been correlated with the general decrease in temperature observed by several studies: a gradual increase in the isotopic $\delta^{18}\text{O}$ values took place [DSDP Sites 608 (Miller *et al.*, 1991) and 588 (Zachos *et al.*, 2001)] during this time-span called the ‘Monterey cooling event’ and is related to the increase in the development of the East Antarctic Ice Sheet (Zachos *et al.*, 2001). The isotopic values also indicate that this cooling dynamic continued during the Late Miocene and Pliocene (Zachos *et al.*, 2001).

Regional vs. global climatic change

The decrease in thermophilous plants and, on the contrary, the noticeable increase in mesothermic plants and altitudinal trees, can be interpreted as a result of the abovementioned climatic cooling, or from the uplift of the surrounding mountains in this area, which was very intense during the studied time period (Kuhlemann, 2007). In both cases, altitudinal elements would increase. However, the estimated climate, using only taxa growing at low to middle-low altitude, seems to confirm a

decrease in mean annual temperatures, which was most likely not sufficient on its own to explain the development of an *Abies–Picea* forest. The two phenomena coexisted, and it is quite difficult to separate one process from the other (global climatic forcing vs. regional relief uplift) due to the tectonic situation of the studied area and the fact that the two may have interacted with one another. What is clear is that even if the uplift of the surrounding mountains may have influenced the regional climate and the increase in conifers observed in the pollen spectra, the evolution of the vegetation during the Miocene was very dependent on the global climatic signal, as shown in previous studies (Ivanov *et al.*, 2002; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005; Mosbrugger *et al.*, 2005; Böhme *et al.*, 2007; Erdei *et al.*, 2007; Utescher *et al.*, 2007).

Palaeoaltitude of the Eastern Alps during the Miocene

Pollen data do not allow us to estimate the altitudinal range of the *Abies* belt, or know whether the alpine herbaceous and perpetual-snow belts above it existed. This is because herbaceous elements from the alpine belt cannot be differentiated from herbaceous taxa growing at lower elevations. Taking this into account, this study shows the following:

- (1) During the Burdigalian, the Eastern Alps were lower than 1800 m. This is in accordance with the structural and sedimentological data from previous studies (Schmid *et al.*, 1996; Frisch *et al.*, 1998; Kuhlemann & Kempf, 2002) that interpret a moderate elevation for the eastern part of the Eastern Alps for the same time period. Kuhlemann (2007) also shows that the proto-Carpathians were most probably elevated below 500 m.
- (2) Palaeoaltitudes of the Eastern Alps increased during the Langhian with estimations higher than 1600 m. This coincides with the palaeogeographical and palaeotopographical reconstructions from Kuhlemann (2007), who demonstrates a rapid uplift of the eastern part of the Eastern Alps and the Carpathians at this time.
- (3) Pollen records from the Serravallian and Tortonian sections indicate an active uplift since the middle Miocene. This increase in high-altitude conifers is also evident in other sections from the Western Alps and Jura (Jiménez-Moreno, 2005).

These estimations coincide with the sedimentological and tectonic interpretations from previous studies in the Eastern Alps that stated that the main uplift took place during the Late Miocene (Frisch *et al.*, 1998) and that an important exhumation rate occurred between 22 and 13 Ma (Hejl, 1997; Dunkl *et al.*, 1998; Kuhlemann *et al.*, 2006). Similar to the Eastern Alps, moderate to rapid uplift created the moderately elevated Carpathian chain in the Late Miocene, partly starting from lowland levels (Kuhlemann, 2007).

CONCLUSIONS

The pollen analysis of sediments from several sections taken from the Central Paratethys in Austria allowed us to charac-

terize the vegetation and climate during the Miocene in this part of Central Europe. It also permitted the reconstruction of palaeoaltitudes of the eastern part of the Eastern Alps during the Early to Middle Miocene.

The abundance of thermophilous elements in the pollen spectra and the high temperature estimations during the Early and early Middle Miocene indicate that the climate was subtropical. This has been correlated with the warmest period during the Miocene: the MCO. During the Serravallian and Tortonian, important changes in the vegetation occurred as several thermophilous elements strongly decreased, many of them disappearing from the Central European region. They were substituted by deciduous and mesothermic plants. This is interpreted as a progressive climatic cooling that is universally known in the literature as the 'Monterey cooling event' and was mainly related to an increase in the volume of the Eastern Antarctic ice sheet.

This study also shows an increase in conifers typical of high elevations (*Cathaya*, *Cedrus*, *Tsuga*, *Picea* and *Abies*) during the Miocene in Austria. This was mainly related to the effects of the intense regional tectonics, generating the uplift of the Alps, as the climatic cooling was certainly not sufficient to develop an *Abies–Picea* forest. Therefore, using a new method based on pollen and climatic data, palaeoaltitudes of the Eastern Alps have been reconstructed. This shows that during the Burdigalian, the Eastern Alps had an altitude of less than 1800 m. Palaeoaltitudes increased during the Langhian with estimations higher than 1600 m. Pollen records from the Serravallian and Tortonian sections indicate an intense uplift during the Middle Miocene. These palaeoaltitude results correspond to minimum values, but show an important increase in elevation during the Early Miocene. They also demonstrate increasing values of palaeoaltitudes in the Eastern Alps due to an increase in the rate of uplift during the Middle and Late Miocene.

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BIOSKETCHES

Gonzalo Jiménez-Moreno works on European Miocene palaeoecological and palaeoclimatic records using pollen and other proxies. He has also conducted several high-resolution pollen studies on Late Pleistocene and Holocene sediments from the USA.

Séverine Fauquette works on climate reconstructions based on pollen data using the 'climatic amplitude method', which she developed. This method has been applied to many pollen sequences from the western Mediterranean area. She has also established a new method for palaeoaltitude estimation using the pollen data.

Jean-Pierre Suc has worked extensively on pollen analysis of the Neogene and Quaternary marine and continental sediments from Europe. He has published more than 100 papers and has supervised more than 20 doctoral students.

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Seasonality intensification and long-term winter cooling as a part of the Late Pliocene climate development

Stefan Klotz ^{a,b,*}, Séverine Fauquette ^c, Nathalie Combourieu-Nebout ^d, Dieter Uhl ^{a,e}, Jean-Pierre Suc ^b, Volker Mosbrugger ^a

^a Institut für Geowissenschaften, Universität Tübingen, Sigwartstr. 10, 72070 Tübingen, Germany

^b Laboratoire PaléoEnvironnements et PaléobioSphère (UMR 5125 CNRS), Université Claude, Bernard- Lyon 1, 27-43 boulevard du 11 Novembre, 69622 Villeurbanne Cedex, France

^c Institut des Sciences de l'Evolution (UMR 5554 CNRS), Université Montpellier II, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France

^d Laboratoire des Sciences du Climat et de l'Environnement (UMR 1572), L'Orme des Merisiers, Centre de Saclay, 91191 Gif-sur-Yvette Cedex, France

^e Laboratory of Palaeobotany and Palynology, Department of Palaeoecology, University of Utrecht, Budapestlaan 4, 3584 CD Utrecht, The Netherlands

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Abstract

A mutual climatic range method is applied to the Mediterranean marine pollen record of Semaforo (Vrica section, Calabria, Italy) covering the period from ~2.46 Ma to ~2.11 Ma. The method yields detailed information on summer, annual and winter temperatures and on precipitation during the nine obliquity and precession-controlled 'glacial' periods (marine isotope stages 96 to 80) and eight 'interglacial' periods (marine isotope stages 95 to 81) characterising this time interval. The reconstruction reveals higher temperatures of at least 2.8 °C in mean annual and 2.2 °C in winter temperatures, and 500 mm in precipitation during the 'interglacials' as compared to the present-day climate in the study area. During the 'glacials', temperatures are generally lower as compared to the present-day climate in the region, but precipitation is equivalent. Along the consecutive 'interglacials', a trend toward a reduction in annual and winter temperatures by more than 2.3 °C, and toward a higher seasonality is observed. Along the consecutive 'glacials', a trend toward a strong reduction in all temperature parameters of at least 1.6 °C is reconstructed. Climatic amplitudes of 'interglacial–glacial' transitions increase from the older to the younger cycles for summer and annual temperatures. The cross-spectral analyses suggest obliquity related warm/humid–cold/dry 'interglacial–glacial' cycles which are superimposed by precession related warm/dry–cold/humid cycles. A time displacement in the development of temperatures and precipitation is indicated for the obliquity band by temperatures generally leading precipitation change at ~4 kyr, and on the precession band of ~9.6 kyr in maximum.

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1. Introduction

Research into the Late Pliocene climate is of especial interest as it contributes to the understanding of

* Corresponding author. Institut für Geowissenschaften, Universität Tübingen, Sigwartstr. 10, 72070 Tübingen Germany. Tel.: +49 7071 2973081; fax: +49 7071 295217.

E-mail address: stefan.klotz@uni-tuebingen.de (S. Klotz).

the nature and the processes of global cooling that evolved since the Miocene and intensified after ~2.8 million years ago, exhibiting an alternation of warm ('interglacial') and cool-temperate ('glacial') periods (e.g., [1–6]). The Late Pliocene palaeoclimate response of the Mediterranean is well documented by marine proxy data [7–11] and few vegetation records [6,12,13]. The marine data revealed the strong influence of the ~41 kyr obliquity periodicity dominantly affecting high latitude climate and leaving its signature in less pronounced 'interglacial–glacial' cycles [14], and the ~23 kyr precession periodicity mainly influencing lower latitude monsoonal activity [11]. Especially, it has been shown that Sea Surface Temperature changes in the Mediterranean were obliquity-controlled and caused by 'interglacial–glacial' variability, whereas Sea Surface Productivity and Salinity changes were precession-controlled and associated with sapropel formation [9,15]. The latter were interpreted as reflecting the influence of the African monsoon. In addition, in a high-resolution marine pollen record of the Semaforo section (Calabria, Italy) covering MIS 96 to 89 (~2.3 to ~2.17 Ma) [5,16], the alternation between warm humid 'interglacials' (obliquity maxima) and cold-temperate dry 'glacials' (obliquity minima) was documented, the cycles of which were assumed to be superimposed by relatively warm humid conditions at times of precession minima and cold dry conditions during precession maxima [15]. So far, however, quantification of terrestrial temperature and precipitation changes on orbital scales are rather sparse for the Late Pliocene, especially in the Mediterranean. The main reason may be first the very few available (relative high-resolution) terrestrial palaeoclimate archives, such as pollen records. In addition, reconstruction methods are required which do not consider modern analogue floras since for older periods (i.e. pre Mid-Pleistocene) frequently floras exist which have no present-day equivalents. Therefore, potentially mutual climatic range methods are applicable (e.g., [17–21]) which determine the ranges of the climatic tolerances of fossil floras by means of the mutual present-day ranges of the nearest living relatives (NLR) of the plants represented in the fossil assemblages. However, so far the climatic resolution is often low with these methods and the databases of the climate requirements of the present-day nearest living relatives of fossil plants are often poor. Hence, we performed a sophisticated mutual climatic range method to provide quantitative temperature and precipitation estimates for the extended data set of the Semaforo pollen record [22] covering the interval of

MIS 96 to 80, and to analyse the reconstruction results for palaeoclimatic characteristics. Specifically, we address the following questions: (1) which main climatic trends related to atmospheric changes characterise the successive Late Pliocene cold and warm phases, and (2) how do the vegetation pattern and the reconstructed climate parameters correspond to the obliquity and precession signals?

2. The marine record of Semaforo and its chronology

The Semaforo section contains a marine record exposed South of Crotona/Italy (39°N, 16°42'E) (Fig. 1). The record consists of 180 m of marine clays, comprising 8 sapropel layers (layers 222 to 204 after Hilgen [14]) and 3 volcanic ash beds (near sapropel layers 222, 208, 206). The time stratigraphic frame of the Semaforo record is well established by astronomically tuned sapropel chronology used for the standard geologic time scale, as well as the standard isotope stratigraphy [15,16,23], suggesting to cover the time span from ~2.46 to ~2.11 Ma (Fig. 2). With respect to the international agreement placing the Pliocene–Pleistocene boundary near the top of the Olduvai subchron at 1.086 Ma as defined in the overlying Vrica section/Italy [23,24], the Semaforo section belongs to the Late Pliocene, the Gelasian Stage. Palynologically, the record is represented in

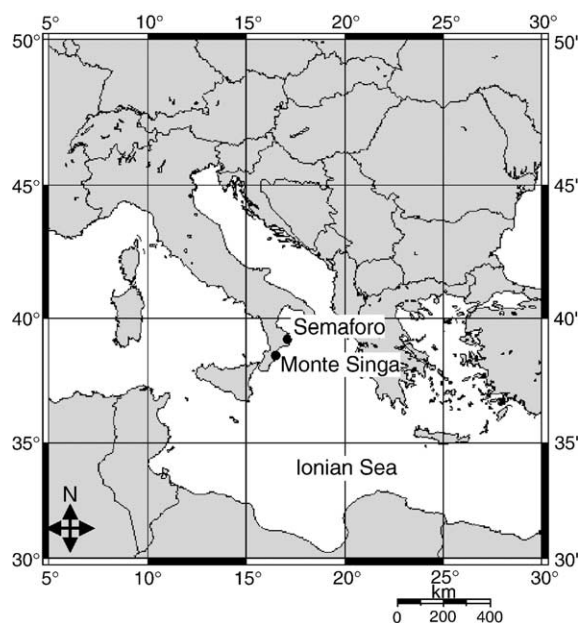


Fig. 1. Site map of the study area with the sections Semaforo and Monte Singa.

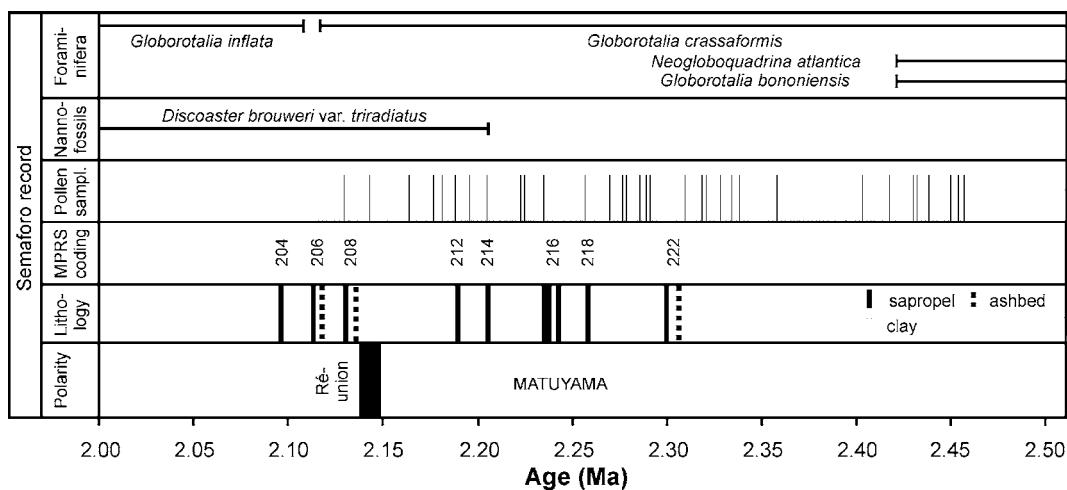


Fig. 2. Stratigraphic column with chronology, polarity zones and lithology [16], MPRS coding [14], pollen samples and biostratigraphy [16].

165 pollen spectra with 110 taxa identified, sampled along 175 m of sediments on intervals between 0.7 and 2 m [16]. For each sample which has been processed according to the standard HF method [25], a number between 200 and 1400 pollen grains have been counted, and abundances have been plotted into a pollen diagram (Fig. 3). The pollen floras sensitively reflect the palaeoclimate development of ‘interglacial–glacial’ cycles during the Late Pliocene by the repetitive alteration of main vegetation units. These units, which are grouped with respect to the phytogeographical affinities of plants, repeatedly change from deciduous forest (main abundant taxa are *Quercus*, *Acer*, *Ilex*, *Carpinus*, *Buxus*, *Eucommia*, *Carya*, *Juglans*, *Pterocarya*, *Ulmus*) to subtropical humid forest (*Cathaya*, *Engelhardia*, *Magnolia*, *Nyssa*, *Symplocos*, *Taxodiaceae*), to altitudinal forest (*Tsuga*, *Cedrus*, *Picea*, *Abies*), and to open herbaceous formation (*Chenopodiaceae*, *Poaceae*, *Artemisia*, *Ephedra*, *Asteraceae*). Another vegetation unit is represented by Mediterranean ecosystems (*Olea*, *Ceratonia*, *Pistacia*, *Quercus ilex*, *Cistus*, *Phillyrea*, *Ligustrum*), which irregularly follows deciduous forest or subtropical humid forest (Fig. 4). From the base to the top of the fossil pollen record, subtropical humid forest elements (especially *Taxodiaceae*) are increasingly replaced by deciduous forest elements (especially *Quercus*), until the subtropical ecosystems finally disappear in the Mediterranean at ~1.2 Ma [5,22]. Simultaneously, a general increase in altitudinal forest elements and *Artemisia* as an indicator for open vegetation is observed, but tree pollen always dominate over herbaceous pollen. Climatically, this pattern has been interpreted to suggest (1) that ‘interglacial’ temperature maxima may decrease during

the course of the Late Pliocene, (2) that aridity or seasonality increases, (3) that ‘glacial’ times experienced enhanced aridity, and (4) that precipitation decreases later than temperatures during ‘interglacial–glacial’ transitions [16,22].

3. Method used for palaeoclimate reconstruction

For a sophisticated interpretation of palaeoclimate signals, the “probability mutual climatic spheres” (PCS) described in detail by Klotz [20] and Klotz et al. [21,28] is applied, taking into account 60 out of 110 taxa identified in the fossil pollen floras for reconstruction (Table 1). The principle of PCS is based on the calculation of palaeoclimate ranges for a fossil flora by means of mutual 2-dimensional climatic spheres of the NLR of the individual plants which participate in the fossil flora. The 2-dimensional spheres representing the present-day climate requirements of the NLR are derived from the correlation of present-day climate data with digitised potential distribution maps of plants. Within the mutual 2-dimensional climatic sphere of a fossil flora, probability intervals are calculated for the individual climate parameters. For explanation, we refer to mean annual temperature (MAT) as an example. First, the range of MAT as inferred from the mutual climatic sphere of the fossil flora is compared to those MAT ranges which have been calculated for 9555 present-day floras, and for which present-day climate data are available. It can be observed that the actual MAT values of those present-day floras which have similar ranges as the fossil flora accumulate within a smaller interval of the total range, indicating the climatic

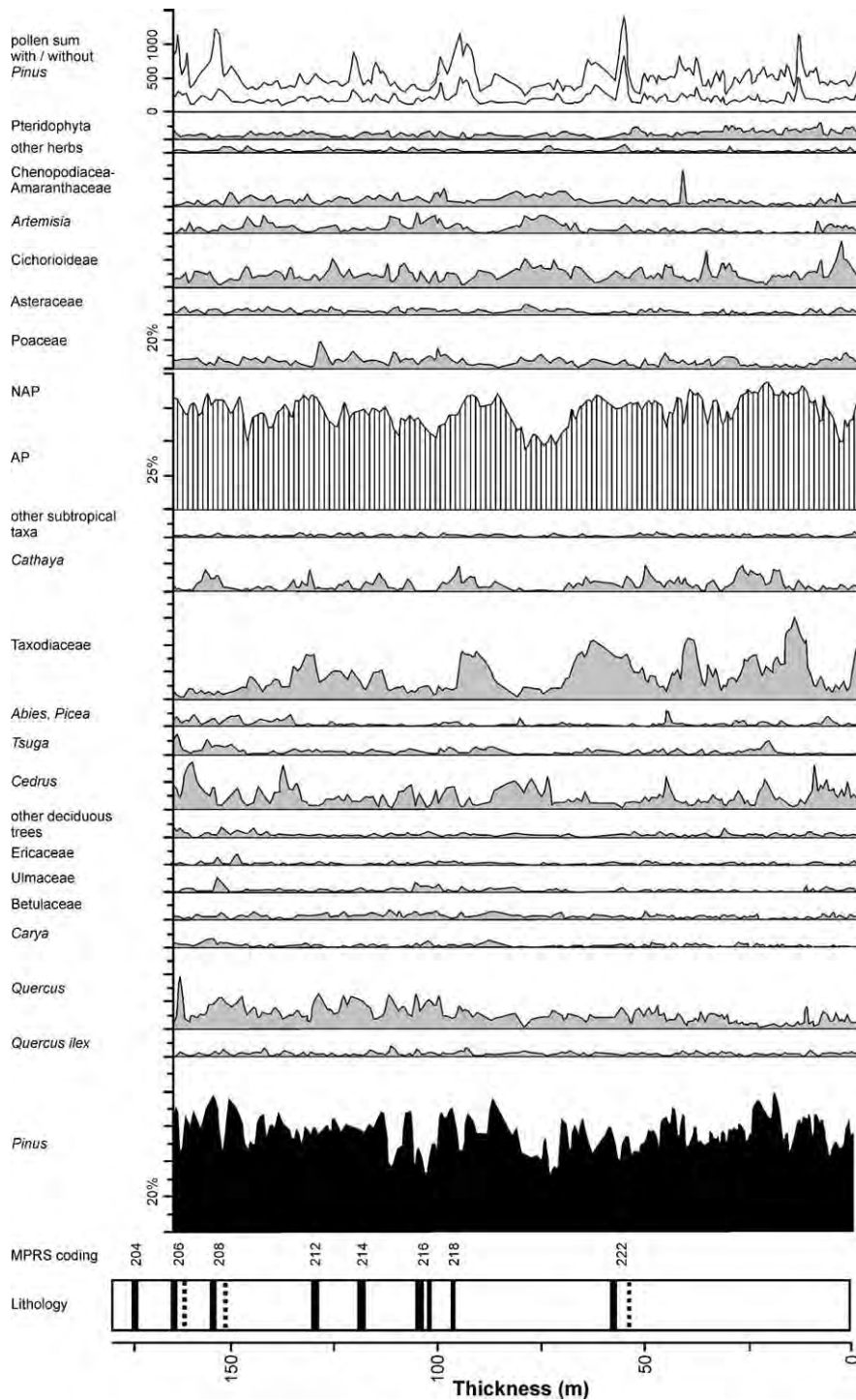


Fig. 3. Pollen diagram of the Semaforo record according to Combourieu-Nebout [22] with thickness, lithology [16] (same caption as in Fig. 2) and MPRS coding [14]. Percentages of *Pinus* are calculated on the total pollen and spores sum, percentages of other taxa and AP, NAP are based on the total sum excluding *Pinus*.

preference of the floras. The interval of preference is then interpreted as the probability interval of MAT. For representation of the reconstructions, we use the

centres of the probability intervals. The quality of PCS has been tested on the base of a multitude of present-day floras [20,21], yielding information on the large

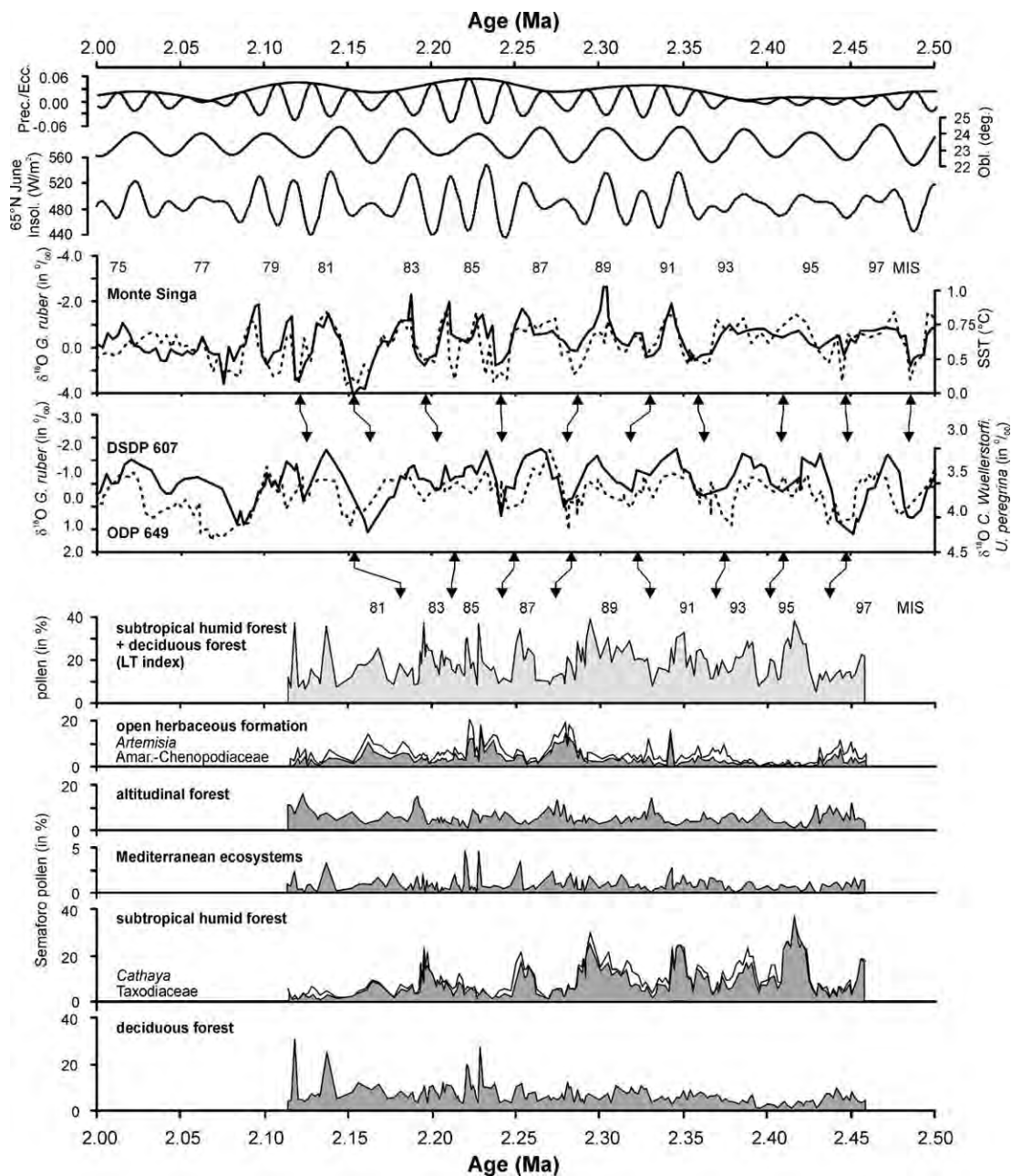


Fig. 4. Generalised pollen diagram of the Semaforo record represented by the percentages of the main vegetation units deciduous forest, subtropical humid forest (most abundant taxa are Taxodiaceae and *Cathaya*), Mediterranean ecosystems, altitudinal forest, and open herbaceous formation (most abundant taxa are Amaranthaceae–Chenopodiaceae and *Artemisia*). Abundance of subtropical humid+deciduous forest reflects a qualitative land temperature (LT) index according to Lourens [15]. Correlation of the Semaforo pollen record with relevant marine indices: The LT index, Sea Surface Temperatures (SST) and planktonic $\delta^{18}\text{O}$ data from the Singa section ($38^{\circ}3'\text{N}$, $16^{\circ}3'\text{W}$, ~100 km South South–West of Semaforo) [9], and benthic $\delta^{18}\text{O}$ record from DSDP 607 in the North Atlantic [1] are tied in the lower section according to Lourens [15] and Lourens et al. [9] identifying marine isotope stages (MIS) 96 to 90. This scheme is continued for the upper section. Correlation is made also with the benthic $\delta^{18}\text{O}$ record from eastern equatorial Pacific site ODP 849 [26] and with orbital signatures [27].

agreement between reconstructed and actual climate values (for which the correlation coefficients and mean aver age error are 0.95, 1.1 °C for summer

temperatures, 0.95, 1.7 °C for winter temperatures, 0.95, 1.1 °C for mean annual temperature, and 0.86, 100 mm for mean annual precipitation, respectively).

Table 1

Pollen taxa identified in the Semaforo record, grouped according to the phytogeographical affinities of the plants [5]

Deciduous forest	Subtropical humid forest	<i>Centaurea</i>	Non classified taxa
• <i>Acer</i>	• <i>Cathaya</i>	Compositae Asteroideae	Abietaceae
• <i>Alnus</i>	<i>Distylium</i>	Compositae Cichorioideae	Araliaceae
• <i>Betula</i>	• <i>Engelhardia</i>	Brassicaceae	• <i>Armeria</i>
• <i>Buxus</i>	<i>Magnolia</i>	• Cyperaceae	Boraginaceae
• <i>Carpinus</i>	• <i>Myrica</i>	• <i>Ephedra</i>	Caprifoliaceae
• <i>Carya</i>	• <i>Nyssa</i>	<i>Lygeum</i>	Convolvulaceae
• <i>Celtis</i>	Palmae	• Poaceae	<i>Euphorbia</i>
• <i>Cornus</i>	Sapotaceae	<i>Phlomis</i>	Euphorbiaceae
• <i>Corylus</i>	<i>Sciadopitys</i>	• <i>Plantago</i>	Gentianaceae
Elaeagnus	• <i>Simplocos</i>	• <i>Rumex</i>	<i>Geranium</i>
• Ericaceae	• Taxodiaceae	Apiaceae	• <i>Helianthemum</i>
• <i>Eucommia</i>	<i>Taxodium</i>	Mediterranean sclerophyllous forest	• <i>Knautia</i>
• <i>Fagus</i>	Altitudinal Coniferous forest	<i>Cerantonia</i>	Lamiaceae
• <i>Hedera</i>	• <i>Abies</i>	<i>Cistus</i>	Fabaceae
• <i>Ilex</i>	• <i>Cedrus</i>	<i>Citrus</i>	<i>Lilium</i>
• <i>Juglans</i>	• <i>Picea</i>	Cupressaceae	Liliaceae
<i>Liquidambar</i>	<i>Tsuga</i>	• <i>Fraxinus</i>	Malvaceae
• <i>Lonicera</i>	Open vegetation	<i>Jasminus</i>	<i>Nolina</i>
• <i>Ostrya</i>	Amaranthaceae	• <i>Ligustrum</i>	Nymphaeaceae
<i>Parrotia</i>	• Chenopodiaceae	Myrtaceae	Fabaceae Papilionioideae
• <i>Platanus</i>	• <i>Artemisia</i>	• <i>Olea</i>	Plumbaginaceae
• <i>Populus</i>	Caryophyllaceae	• <i>Phillyrea</i>	• <i>Potamogeton</i>
• <i>Pterocarya</i>		• <i>Pinus</i>	Ranunculaceae
• <i>Quercus</i>		• <i>Pistacia</i>	Rosaceae
• <i>Salix</i>		• <i>Quercus ilex type</i>	<i>Rhus</i>
• <i>Sambucus</i>		• <i>Rhamnus</i>	Solanaceae
Taxaceae			• <i>Sparganium</i>
• <i>Tilia</i>			Tymeleaceae
• <i>Ulmus</i>			<i>Typha</i>
• <i>Vitis</i>			Valerianaceae
• <i>Zelkova</i>			

Dots indicate those taxa which are used for palaeoclimate reconstruction.

Specifically, the high correlation coefficients indicate that PCS is able to reliably reproduce trends.

4. Late Pliocene climate

The application of PCS on the Semaforo pollen record allows a detailed view on the Late Pliocene climate development in the Mediterranean, revealing the succession of eight ‘interglacials’ and nine ‘glacials’ (Fig. 5). Changes in temperature parameters are mostly correlated with each other ($R^2 > 0.67$, $p < 0.01$), whereas temperature parameters and precipitation are autocorrelated (temperatures leading by ~4 kyr, $R^2 > 0.47$, $p < 0.01$). As compared to temperature parameters, precipitation shows larger relative fluctuations during ‘interglacials’. Generally, average oscillations in the transition between ‘interglacials’ and ‘glacials’ are higher in mean temperatures of the coldest month (MTC, 7.3 °C) than in mean annual temperatures (MAT, 6.6 °C) and in mean temperatures of the coldest month (MTW, 5.3 °C); mean annual

precipitation (MAP) shows an average range of 540 mm. Maximum summer temperatures during the consecutive ‘interglacials’ vary between 23.8 and 25.1 °C, annual temperatures between 13.2 and 15.5 °C, winter temperatures between 8.0 and 10 °C, and annual precipitation between 985 and 1444 mm. Lowest seasonality and highest oceanicity is revealed for MIS 95 (MTW-MTC is 14.6 °C, MAP is 1444 mm), highest continentality for MIS 81 (MTW-MTC is 16.5 °C). As compared to the present-day climate at Semaforo, during MIS 95, MTW is 2.4 °C, MAT is 1.9 °C, MTC is 3.3 °C, and MAP is 600 mm higher (note that the reconstructions integrates also the climatic signals from high altitude forest elements). Climate conditions during MIS 95 may be most similar to those at present of some regions in Central South China (~24° to 27°N, ~102° to 107°E) and South-Eastern South America (~32° to 36°S, ~54° to 61°E), both regions which are strongly influenced by seasonal reversal (monsoonal) winds. Minimum summer temperatures during the consecutive ‘glacials’ vary

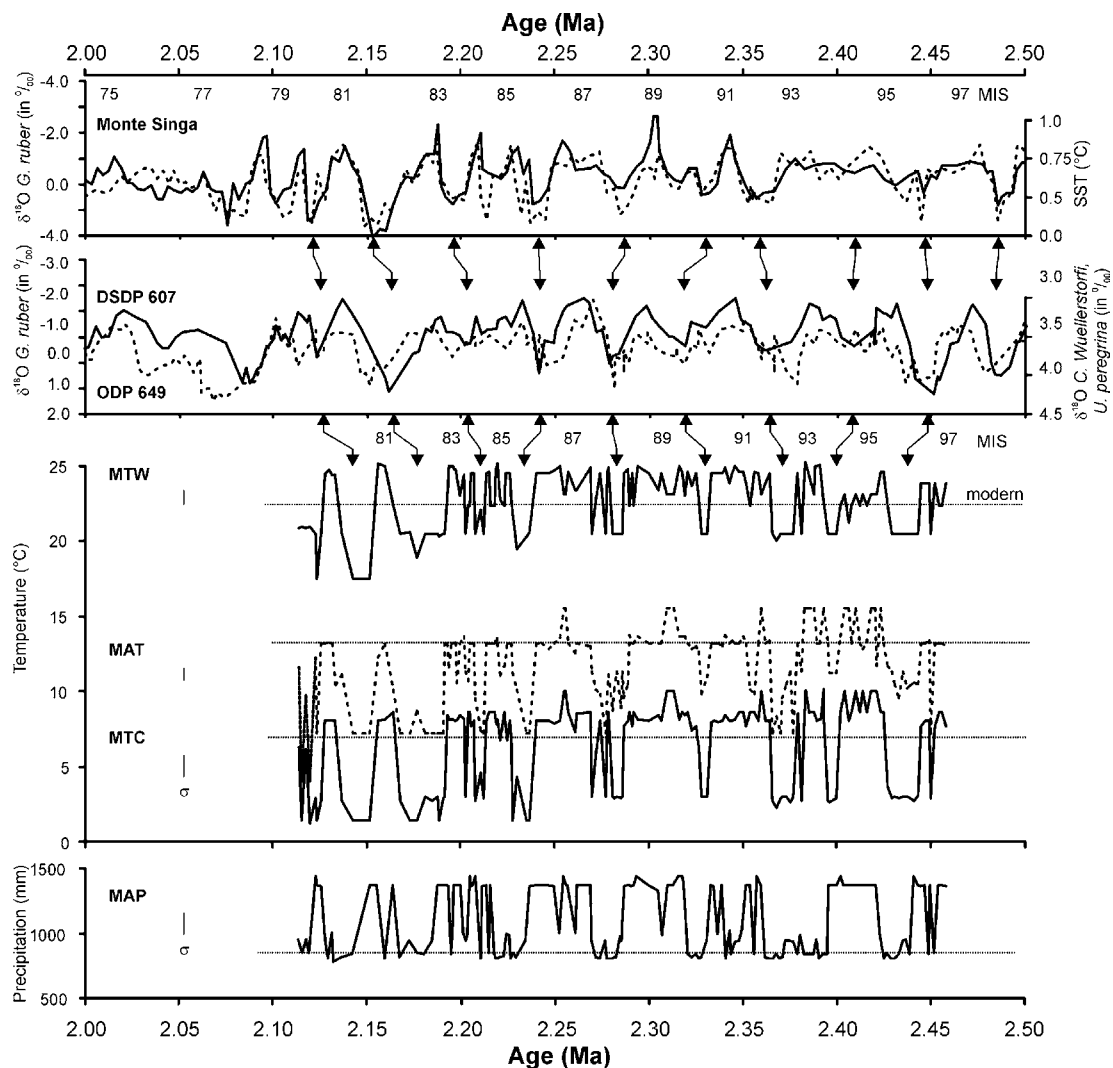


Fig. 5. Climate reconstruction with the PCS method for the Semaforo pollen record, represented by the centres of the mutual climatic ranges for the parameters mean temperature of the warmest month (MTW), mean annual temperature (MAT), mean temperature of the coldest month (MTC) and mean annual precipitation (MAP). Note that although the centres of the probability intervals of PCS point to specific values, it is emphasised that the method basically provides intervals reflecting the ranges of actual palaeoclimate data. Standard deviation (σ) from the centres is 1 °C for MTW, 0.67 °C for MAT, 0.9 °C for MTC, and 166 mm for MAP. Modern climate data at Semaforo (MTW 22.2 °C, MAT 13.6 °C, MTC 6.7 °C and MAP 850 mm) are shown on figure, represented by dotted vertical lines. The climate record is shown together with the planktonic $\delta^{18}\text{O}$ record, marine isotope stages (MIS), and sea surface temperatures from the Singa section [9], with the benthic $\delta^{18}\text{O}$ record from DSDP 607 [1] and eastern equatorial Pacific site ODP 849 [26], with obliquity and with precession modulated 65°N June insolation [27].

between 17.5 and 20.5 °C, annual temperatures between 7.2 and 11.2 °C, winter temperatures between 1.4 and 3 °C, and annual precipitation between 780 and 990 mm. Lowest summer, annual, and winter temperatures are found for MIS 80 (MTW-MTC is 16.1 °C). As compared to the present-day climate at Semaforo, during MIS 80, MTW is 4.7 °C, MAT is 6.4 °C, MTC is 5.3 °C, and MAP is 70 mm lower. Climate conditions during MIS 80 may be most sim-

ilar to those at present of some regions in South France (~44° to 47°N, ~2° to 5°E) and Central West Italy (~42° to 44°N, ~12° to 13°E). The reconstructed values for the 'interglacials' and 'glacials' are reasonably in agreement with estimates for the Mediterranean pollen record of Garraf 1, northeastern Spain [19,29], covering the time window ~5.3 to ~1.75 Ma in 48 pollen samples (10 samples during ~2.5 to ~2 Ma). The deviations between the reconstructed aver-

Table 2

Present-day climate conditions at the localities of Semaforo and Garraf 1 (41°10'N, 2°01'E) with respect to the mean temperature of the warmest (MTW) and coldest month (MTC) in °C, and mean annual precipitation (MAP) in mm

		MTW	MTC	MAP
Present-day	Semaforo	22.2	6.7	850
	Garraf 1	21.4	6.5	690
	gradient S-G	−0.8	−0.2	−160
'Interglacials' maxima	Semaforo	25.0	9.5	1370
	Garraf 1	25.7	9.2	1100
'Glacials' minima	Semaforo	19.8	2.3	830
	Garraf 1	22.0	1.0	600

Average values are calculated for the maxima of the 'interglacials' and minima of the 'glacials' for both records.

age climate values at Garraf 1 and Semaforo largely correspond to the present-day climate gradient between these localities (Table 2). Hence, our reconstructions for that period reflect broad regional climatic patterns.

5. Discussion

The Semaforo pollen record provides an excellent opportunity for the study of the Mediterranean vegetation and climate response on orbital forcing during the Late Pliocene within the time window ~2.46 to ~2.11 Ma. The cyclic vegetation changes recorded in the Semaforo sequence have been proposed to result mainly from variations in temperature and moisture [22,30], affecting shifts in vegetation belts over the Sila Massif 30 km North of Semaforo (palaeoaltitude more than 1500 m [31]) which represents the main pollen source area [32]. In this regard, the change from subtropical forests to open herbaceous formation would reflect the shift from warm and humid 'interglacials' to cold and/or dry 'glacials'. The potential influence of an uplift of the Sila Massif (today 2000 m in altitude) on exposing larger areas for open vegetation (or altitudinal forest) which could influence the palaeoclimate reconstruction, can mostly be disregarded since (1) a constant uplift during the past ~2.46 Ma would result in an uplift of ~70 m during the period covered by the Semaforo record, and (2) there is evidence that the uplift took place after the deposition of marine terraces during or after the middle Pleistocene since these terraces have protected the Semaforo section after its outcrop. Using the PCS method for interpretation of the palaeoclimatic signals reflected by the vegetation, detailed in formation is provided for temperature and precipitation change, suggesting general trends along the successive 'interglacials' and 'glacials'.

5.1. Relationship to orbital parameters and $\delta^{18}\text{O}$ data

The spectral analyses on selected vegetation units and on groupings reveal that the vegetation largely responded to the orbital forcing of the ~41 and ~23 kyr periodicities, whereas the ~100 kyr component is weak (Fig. 6a). Interestingly, the obliquity signal is best reflected by subtropical humid forest, altitudinal forest and open herbaceous vegetation, the first of which is also showing a precession component. In contrast, from all the vegetation units, Mediterranean ecosystems and deciduous forest show strongest response to the precession band. With view on groupings of vegetation units (subtropical humid forest+deciduous forest, and subtropical humid forest+altitudinal forest), combined effects are observed in that the spectral patterns of these groups are largely determined by the interference of the spectral patterns of the individual vegetation units. Concerning the reconstructed climatic parameters which interpret the vegetation signals, the spectral analysis suggests a strong control of the ~41 kyr periodicity on variations in temperatures and notably also in precipitation. In contrast, the ~23 kyr periodicity operates stronger on precipitation changes than on temperatures. (Fig. 6b).

5.1.1. Obliquity forcing

The obliquity controlled variations in the Semaforo record, and in the $\delta^{18}\text{O}$ data and Sea Surface Temperatures from the Singa section can easily be correlated with the $\delta^{18}\text{O}$ records of sites DSDP 607 and ODP 849 (see Fig. 5), therefore arguing to reflect 'interglacial–glacial' cycles bound to ice volume [9]. Based on cross-spectral analysis, the calculated phase relationships reveal that maximum obliquity is closely related to the abundance of warm humid vegetation elements, and to the maxima of pollen derived climate parameters and Singa SST (Fig. 7). For exact phase angles and coherence see Table 3. As a specific pattern, precipitation lags temperature parameters which may be easily seen by comparison of winter temperatures and precipitation for MIS 95, 91, 89, 85 and 83 (Fig. 6). This finding is in agreement with the palynological evidence [16], suggesting warm/dry conditions during the onset of 'interglacials' by the rise of deciduous forest elements, and cold/humid conditions during the onset of 'glacials' by the rise of altitudinal forest elements. If calculating the mean time displacement in the development especially between winter temperatures and precipitation along the 'glacial–interglacial' transitions MIS 96/95 to 82/81 (time of each first sample is taken independently for winter temperatures and precipitation, when

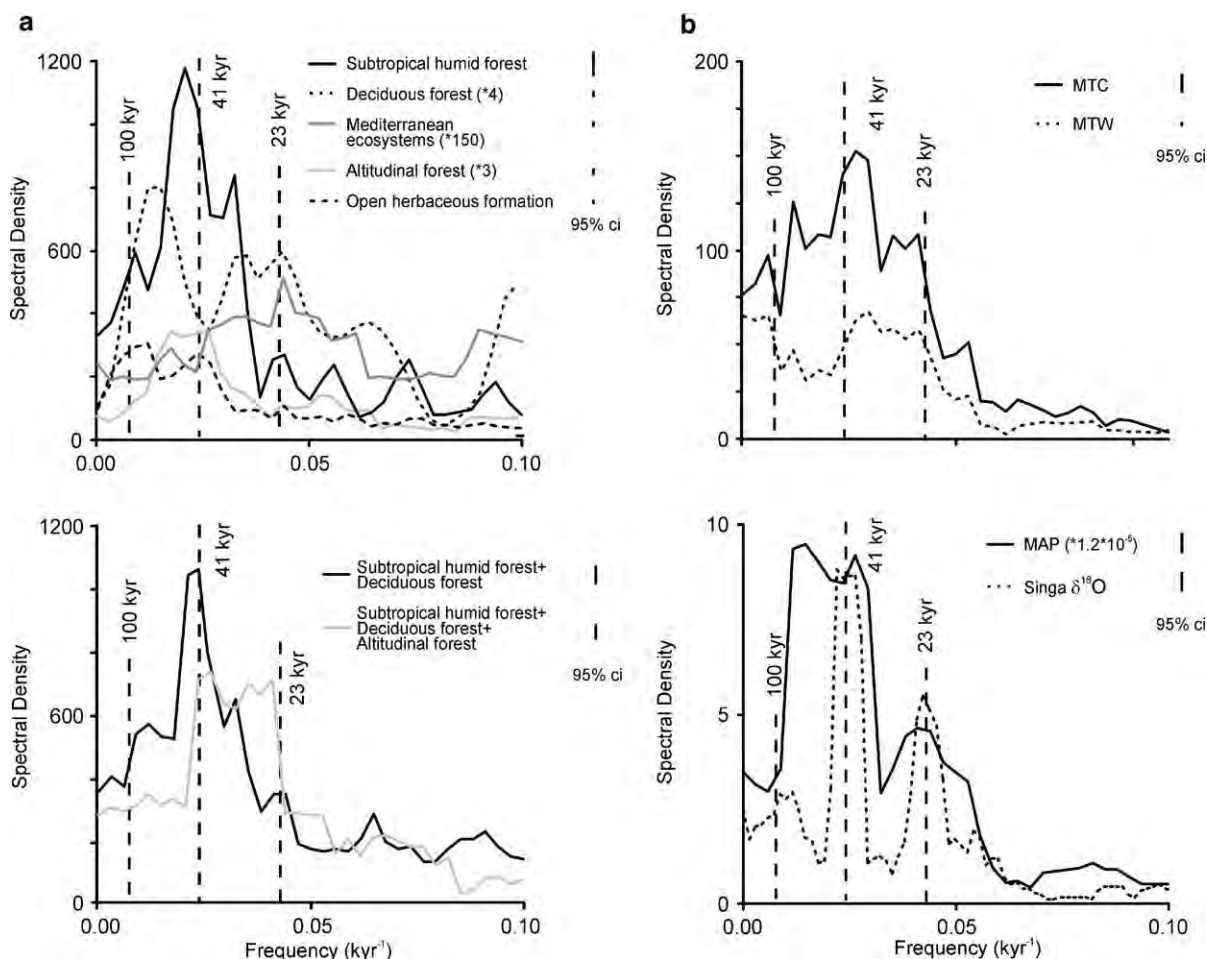


Fig. 6. Power spectra using fast Fourier transformation for different filtered parameters (5% tapered, 7 band Tukey-window). a) Left panel with power spectra for the vegetation units subtropical humid forest, deciduous forest, Mediterranean ecosystems, altitudinal forest and open herbaceous formation, and on the groups. subtropical+deciduous forest and subtropical humid+deciduous+altitudinal forest. b) Right panel with power spectra for the climate parameters mean temperatures of the warmest (MTW) and coldest month (MTC), for mean annual precipitation (MAP), and planktonic $\delta^{18}\text{O}$ data from the Singa section for comparison [9]. Confidence intervals (ci) for the parameters shown on figure.

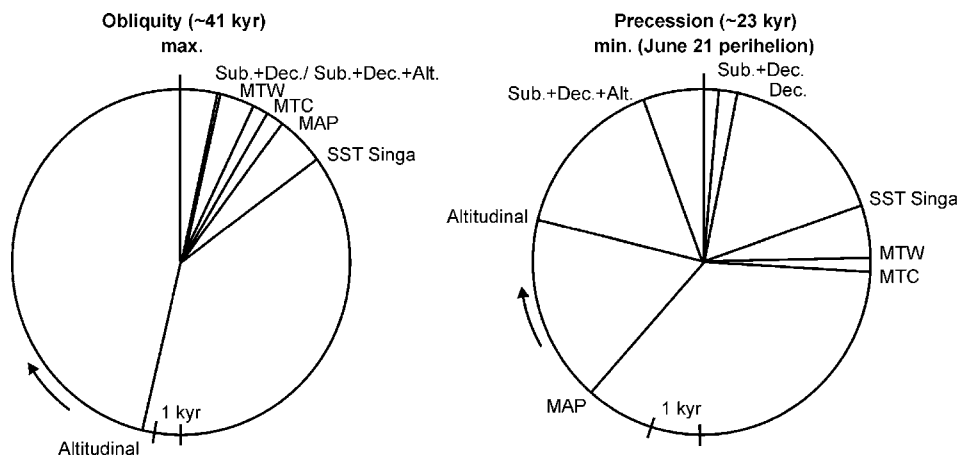


Fig. 7. Cross-spectral analyses using fast Fourier transformation for different filtered parameters (5% tapered, 7 band Tukey-window). Left panel: wheel phase spectrum including different vegetation units, groupings of them, and climate parameter related to obliquity. Right panel: the same for precession.

Table 3

Phase angles in degree (deg.) for the different parameters against obliquity and precession, and coherency (k) (at 95% confidence level)

Parameter	~41 kyr		~23 kyr	
	deg.	k	deg.	k
Subtropical	-12 ± 8	0.87	173 ± 24	0.16
Deciduous	-18 ± 10	0.62	170 ± 3	0.62
Mediterranean	-45 ± 7	0.56	81 ± 3	0.76
Altitudinal	167 ± 3	0.91	-104 ± 2	0.66
Open	156 ± 20	0.47	-173 ± 3	0.37
Sub.+Dec.	-12 ± 4	0.76	175 ± 10	0.49
Sub.+Dec.+Alt.	-12 ± 6	0.73	-162 ± 9	0.61
SST Singa	-52 ± 4	0.41	110 ± 1	0.97
MTC	-30 ± 1	0.69	88 ± 2	0.85
MTW	-25 ± 5	0.66	91 ± 4	0.91
MAP	-37 ± 13	0.59	-41 ± 22	0.96

Parameters include subtropical humid forest (Subtropical, Sub.), deciduous forest (Deciduous, Dec.), Mediterranean ecosystems (Mediterranean), altitudinal forest (Altitudinal, Alt.), open herbaceous formation (Open), Sea Surface Temperatures of the Singa record (SST Singa), mean temperatures of the coldest (MTC) and warmest month (MTW), and mean annual precipitation (MAP).

8 °C and 1360 mm levels defining the ‘interglacials’ “plateaus” are exceeded), a value of ~4.0 kyr is obtained (standard deviation ~3.2 kyr, mean time resolution during these transitions is ~1.7 kyr). For the mean time displacement calculated on the consecutive ‘interglacial–glacial’ transitions MIS 95/94 to 81/80 (when parameter values are below 8 °C and 1360 mm levels), a value of ~3.3 kyr is obtained (standard deviation ~2.0 kyr, mean time resolution during these transitions is ~1.2 kyr). These time lags correspond also to the results provided by a cross-spectral analysis on MTC and MAP, yielding a general phase relationship between these parameters on the obliquity band of $\sim 3.9 \pm 0.4$ kyr (coherency of 0.9). The time lag between precipitation and temperatures can mainly be explained by means of the SST. During the onset of ‘interglacials’ sea surface evaporation influencing precipitation is low due to still cool SST, whereas during the onset of ‘glacials’ still considerable SST allow higher evaporation and precipitation, also supported by lower saturation vapor pressure of the air.

5.1.2. Precession forcing

Since the precession component reflected by the Mediterranean records is almost absent in the $\delta^{18}\text{O}$ data of sites DSDP 607 and ODP 849, it can not be interpreted in terms of ice volume changes but was linked to increased Sea Surface Temperatures (SST) at times of sapropel formation related to variations in freshwater input [9,15]. In contrast to the cyclic patterns related to obliquity, the calculated phase relationships

on the precession band indicate that precipitation is considerably leading minimum precession (maximum insolation), and is more phase related to altitudinal forest and more in anti-phase with SST, MTW and MTC.

According to the cross-spectral analyses, the maximum phase lag of MAP behind MTC is ~9.6 kyr (coherency of 0.73). As a generalised result, the precession related cycles are determined by the alternation of warm/dry–cold/humid phases. This view deviates from the classical (qualitative) pattern of precession related warm/humid–cold/dry cycles [15]. Our results especially suggest that precession related maximum precipitation mainly corresponds to times of generally low temperatures, which may be explained by (1) increased advection and a presumably more northwestern cyclonic wind regime, and/or (2) enhanced relative humidity due to lower saturation vapor pressure of the colder air.

As a general scheme of the palaeoclimatic development during the period covered by the Semaforo record, it has been considered that the obliquity related warm/humid–cold/dry cycles are superimposed by the precession related warm/dry–cold/humid cycles.

5.2. Long-term climatic trends

The reconstructed climate data are analysed for general trends calculating linear regressions for climate parameters along the eight ‘interglacials’ and nine ‘glacials’, that is for the development of ‘interglacial’ maxima, ‘glacial’ minima, and ‘interglacial–glacial’ amplitudes. Unlike the various marine palaeoclimate indices which reveal no obvious characteristics along MIS 97 to MIS 80, the vegetation based climatic analysis suggests different long-term trends of atmospheric change in the Mediterranean.

5.2.1. Annual and winter cooling along consecutive ‘interglacials’

The coldest ‘interglacial’ MIS 81 is even warmer in summer temperatures of ~3 °C, in winter temperatures of ~2 °C, and with higher precipitation of ~500 mm than the modern climate conditions at Semaforo. Referring to the analysis of the ‘interglacials’ maxima along MIS 95 to 81 (total period of ~280 kyr), strong trends of decreasing annual temperatures of ~2.8 °C and winter temperatures of ~2.3 °C become obvious (Fig. 8a). Due to similar summer temperatures, seasonality is increasing during the consecutive ‘interglacials’ by ~2.3 °C. Although the general decrease of subtropical humid elements and their replacement by decidu-

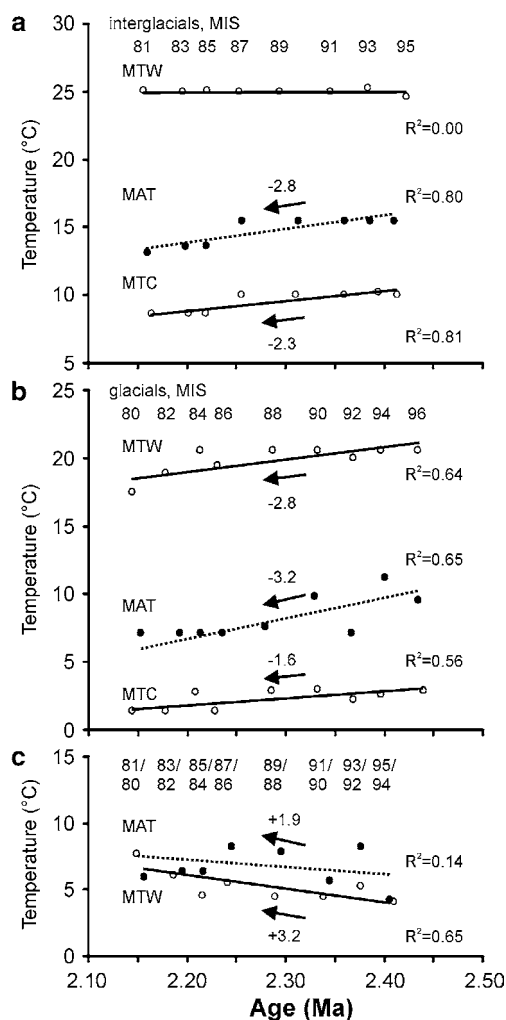


Fig. 8. Linear climatic trends along the consecutive 'interglacials' MIS 97 to 81 and 'glacials' MIS 96 to 80 in the Semaforo record for the parameters mean temperature of the warmest month (MTW), mean annual temperature (MAT) and mean temperature of the coldest month (MTC), related to timescale. (a) Maximum values during the 'interglacials'. (b) Minimum values during the 'glacials'. Coefficients of determination (at significance level $p < 0.01$) for regressions, and resulting total changes between the lower and upper part of the record are shown on figure. (c) Maximum 'interglacial-glacial' amplitudes (difference between 'interglacial' maximum and succeeding 'glacial' minimum values).

ous forest elements [22], the annual precipitation shows no trend. This can be explained by the following: (1) the occurrence of subtropical humid elements during all 'interglacials' (abundance > 6%) indicate warm and (year-long) humid climate conditions at all [5,19,33–36]. (2) The subtropical humid elements are more sensitive to temperature changes rather than precipitation changes, as can be interpreted from the Semaforo and Vrica composite section (Crotone, Italy) spanning the period from ~2.4 to ~1.2 Ma. There, Taxodiaceae

are gradually replaced by *Cathaya* between ~2.4 and ~2.0 Ma, and *Cathaya* is replaced by *Tsuga* after ~1.4 Ma [5,30]. Today, however, these taxa can be found at different altitudes with *Cathaya* and *Tsuga* at higher levels than Taxodiaceae, but all requiring similar levels of high humidity. The finding of decreasing winter temperatures is further in agreement with estimates derived from the northern German record of Lieth (53°43'N, 9°38'E) covering MIS 97 to 81 in about 49 pollen samples, based on the same reconstruction method [37]. It has been proposed for Lieth a gradual decrease in winter temperatures of ~5 °C during the consecutive 'interglacials', and also an increase in summer temperatures of ~1 °C. Regardless of the difference in the reconstructed absolute decreases in winter temperatures at Semaforo and Lieth, the comparison emphasises the over-regional character of the determined trend along the consecutive 'interglacials' during the period considered.

5.2.2. General cooling along consecutive 'glacials'

Strong cooling trends are also observed along 'glacials' MIS 96 to 80 (period of ~300 kyr) for all temperature parameters, with decreasing summer temperatures of 2.8 °C, mean annual temperatures of 3.2 °C, and winter temperatures of 1.6 °C (Fig. 8b). This finding coincides with the general increase of altitudinal forest elements and open vegetation elements, but does not reveal enhanced aridity. Considering the different marine indices, only the $\delta^{18}\text{O}$ data from the Singa record exhibits a weak trend of increasing values along MIS 96 to MIS 78 (+1.3‰, $R^2 = 0.4$). Our results are also in agreement with the pollen based reconstructions from the record of Lieth, where a decrease in winter temperatures of ~5.5 °C along MIS 96 to 80 is suggested [37]. The intensified cooling during the consecutive obliquity dominated 'glacials' may correspond to the strong imprint of the obliquity signal caused by the control meridional temperature gradients exert on the poleward transport of moisture, allowing to progressively build-up Northern Hemisphere ice sheets [38]. It may also be related to intensified atmospheric circulation [39], or to enhanced ice-rafting as evidenced from records in the Norwegian Sea and North Atlantic during 'glacials' and 'interglacial-glacial' transitions [40].

5.2.3. Increasing amplitudes of consecutive 'interglacial-glacial' transitions

Calculating the maximum climatic amplitudes between consecutive 'interglacials' (maximum values are considered) and 'glacials' (minimum values are considered), another trend suggests increasing summer tem-

perature amplitudes of ~ 3.2 °C and mean annual temperatures of ~ 1.9 °C along MIS 96/95 to 81/80 (Fig. 8c). For comparison, the analysis on the $\delta^{18}\text{O}$ data from the Singa record reveals a trend suggesting higher amplitudes along MIS 97/96 to MIS 79/78 ($+2.4\%$, $R^2=0.6$), which is not obvious from the $\delta^{18}\text{O}$ record at DSDP 607 in the North Atlantic. It is especially suggested that changes in global ice volume associated with reductions in the Mediterranean surface-water salinity (resulting from changes in the rates of evaporation/precipitation and from fluvial runoff), led to higher ‘interglacial–glacial’ amplitudes in the region [41,42]. As compared to the amplitude of winter temperature change of more than 18 °C during the last ‘interglacial–glacial’ transition (Eemian–Weichselian) as reconstructed from the pollen record of Lago Grande di Monticchio/Southern Italy [43], the Late Pliocene transitions show less than half in amplitude.

6. Conclusions

The quantitative climate analysis of the Mediterranean pollen record of Semaforo/Southern Italy provides new and detailed information on the climate development along eight Late Pliocene ‘interglacials’ and nine ‘glacials’ during the time window 2.46–2.11 Ma. Mainly forced by the obliquity and the precession signal modulating 65°N June insolation, the analysis of climate development reveals specific characteristics of change.

- (1) Summer, mean annual and winter temperatures, as well as precipitation are considerably higher during the Late Pliocene subtropical humid ‘interglacials’ as compared to present-day climate conditions in the study area. Temperatures during ‘glacial’ periods are lower, but precipitation is similar than at present.
- (2) Relying on the timescale of the Semaforo record, the spectral analyses on vegetation units and on reconstructed climate parameters reveals the considerable imprint of the ~ 41 kyr obliquity and ~ 23 kyr precession periodicity. Generalised, it is evidenced the alternation of warm/humid–cold/dry ‘interglacial–glacial’ cycles on the obliquity band, which are superimposed by warm/dry–cold/humid cycles on the precession band. Whereas the obliquity bound climatic cycles in the Mediterranean largely follows the global change in ice volume, the precession related cycles may be best explained by the influence of warm/dry southern anticyclonic wind circulation alternating with a cold/humid northwestern cyclonic wind regime.

- (3) A time lag of ~ 4 kyr is observed in the development of temperatures and precipitation during the obliquity controlled ‘glacial–interglacial’ cycles, and of ~ 9.6 kyr in maximum during the precession related cycles, with precipitation lagging temperature parameters. Transitional phases are thus characterised by warm/dry or cold/humid conditions.
- (4) Along the consecutive ‘interglacials’ no precipitation trend change is yielded according to the abundance of taxa requiring a high amount of year-long humidity.
- (5) A strong trend in the climate development of over-regional scale along the consecutive Late Pliocene ‘interglacials’ is indicated by the reduction in minimum mean annual and winter temperatures, and by the intensification of seasonality.
- (6) A further trend in the climate development along the consecutive ‘glacials’ is indicated by reduced minimum summer, mean annual, and winter temperatures.
- (7) Considering maximum temperature shifts along the consecutive ‘interglacial–glacial’ transitions, the amplitudes are increasing for summer and mean annual temperatures. As compared to the amplitude of winter temperature change during the last ‘interglacial–glacial’ (Eemian–Weichselian) transition in South Italy, the Late Pliocene shifts are less than half in size.

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The use of pollen floras as a tool to estimate palaeoaltitude of mountains: The eastern Pyrenees in the Late Neogene, a case study

Jean-Pierre Suc ^{a,*}, Séverine Fauquette ^b

^a Institut des Sciences de la Terre de Paris (UMR 7193 CNRS), Université Pierre et Marie Curie, 4 place Jussieu, case 117, 75252 Paris Cedex 05, France

^b Institut des Sciences de l'Évolution de Montpellier, UMR CNRS 5554, Equipe Paléoenvironnements, case courrier 061, Université de Montpellier 2, Place Eugène Bataillon, 34 095 Montpellier cedex 05, France

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ABSTRACT

Northern Hemisphere vegetation is generally zoned as a consequence of latitudinal and altitudinal gradients. Temperature reconstruction from three successive pollen floral assemblages (of Tortonian, Messinian and Zanclean age) from the eastern Pyrenees has been used to estimate the altitudinal evolution of the uplifted Cerdanya Basin and its surrounding massifs. A new method has been developed for the uplifted basins, which completes that already applied to pollen floras from coastal marine deposits close to mountains. In contrast to previous hypotheses, it seems that the eastern Pyrenees occurred at a lower altitude in the Late Miocene before continuous uplift began 10 Ma ago. The rate of this uplift ranged between 0.06 and 0.12 mm/yr.

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1. Introduction

The estimate of palaeoaltitude of mountain belts and its change with time is essential for deciphering movements of the earth surface caused by tectonics, mantle dynamics or climate. It is also essential for placing limits on erosion rates and terrigenous fluxes into sedimentary basins, the reconstruction of vegetation palaeomaps and the development of palaeoclimate models.

Different indirect approaches are used to estimate palaeoaltitudes with equivocal results: some of which provide evidence on denudation, such as thermochronometry (Gunnell, 2000) and geomorphology (Kooi and Beaumont, 1996; Babault et al., 2005). These depend in part on altitude; whilst others provide evidence on the physical conditions of water inclusions within newly crystallised minerals (Chamberlain and Poage, 2000) or those of carbonate precipitation (Mulch et al., 2004). These variables depend on both climate and relief. However, none of these methods considered alone can be used to indicate the true palaeoaltitude evolution of the earth surface.

Present-day vegetation changes according to latitude and altitude, with an almost constant variation with respect to decrease in temperature throughout the Northern Hemisphere, from the south to the north (Troll, 1966, 1973; Ozenda, 2002). As a consequence, plant remains may be used to estimate palaeoaltitudes. This was first applied in Northwestern America using plant macroremains frequently recorded along altitudinal gradients (Axelrod, 1965, 1968; Axelrod

and Bailey, 1976; Meyer, 1992; Wolfe, 1995) using a relatively complex method in the absence of a calculated standard thermal gradient. The passage from thermophilous to boreal forests and the tundra is forced by decreasing mean annual air temperature (MAT). This regulates the thermal classification of plants (Nix, 1982): equatorial then tropical forests, inhabited by megathermic plants ($MAT > 24\text{ °C}$), are gradually replaced by subtropical forests composed of mega-mesothermic plants ($20\text{ °C} < MAT < 24\text{ °C}$), warm-temperate forests composed of mesothermic plants ($14\text{ °C} < MAT < 20\text{ °C}$), mixed and coniferous forests composed of meso-microthermic ($12\text{ °C} < MAT < 14\text{ °C}$) then microthermic plants ($MAT < 12\text{ °C}$), and finally by tundra (composed of microthermic herbs and some dwarf woody elements) that is terminated by snow and ice-dominated climates. This organisation of vegetation was used by Ozenda (1975, 1989, 2002) who succeeded in establishing a standard relationship between the latitudinal and altitudinal thermal gradients. This author took average values for the Northern Hemisphere: 0.60 °C per degree of latitude and 0.55 °C per 100 m in altitude despite slight variability resulting from sunshine exposure. However, establishing such a latitudinal–altitudinal standard thermal gradient for the Northern Hemisphere left open new prospects for palaeoaltitude estimates using plant remains.

Pollen floras, which are generally more abundant than those of plant macrofossil assemblages, provide a broader overview of the vegetation both in latitude and altitude (Suc, 1989). Pollen data seem to provide an efficient tool, with a large potential geographical interest, since they may be extracted both from sedimentary foreland basins and uplifted intra-mountainous basins. An initial method has been developed for low altitude and coastal marine sediments located near massifs (Fauquette et al., 1999). This is based on quantification

* Corresponding author.

E-mail addresses: jeanpierre.suc@gmail.com (J.-P. Suc), severine.fauquette@univ-montp2.fr (S. Fauquette).

of past mean annual temperature (MAT), and using the past latitudinal and altitudinal thermal gradients and latitudinal versus altitudinal distribution of meso–microthermic (i.e. cool–temperate) and microthermic (i.e. boreal) trees. However, this approach only provides an estimate of the minimum palaeoaltitude of the massif because it concerns the lower limit of the highest forest belt. Imprecision is accentuated when a herbaceous belt covered the most elevated part of the massif (pollen analysis is not yet able to detect altitudinal meadows) and more amplified where the summit was continuously covered by ice.

The Neogene latitudinal thermal gradient has been calculated for Europe and the Mediterranean region using pollen records: it is 0.48 °C per degree of latitude for the Middle Miocene, 0.6 °C per degree of latitude since the early Tortonian (Upper Miocene) (Fauquette et al., 2007). The ‘modern-aspect’ reconstructed gradient from pollen floras for the end of the Neogene is consistent with model simulations in particular for the Pliocene (Haywood et al., 2000a, 2000b; Jost et al., 2009).

In this paper, we present a new method based on pollen records from sediments uplifted following deposition. The estimated altitude of massifs is, in the case of the Late Neogene of the eastern Pyrenees, compared to that obtained using the method for low altitude and coastal sediments (Fauquette et al., 1999).

2. The eastern Pyrenees and the study basins

The formation of the Pyrenees follows a complex tectonic history that began in the Palaeozoic, in relation to compressional deformation and metamorphism in the Pyrenean Axial Range (Arthaud and Matte, 1975). The Hercynian chain was then largely eroded, until the Cretaceous. At about 90 Ma, the Iberian Plate moved along a left-lateral strike-slip fault relative to the European Plate as a result of deep-seated modification of the Atlantic Ocean (Olivet, 1996). This plate boundary is represented by the North Pyrenean Fault (Fig. 1B). The Pyrenean orogen grew from the Late Cretaceous to the Early Miocene as a result of the collision between the Iberian and the European plates (e.g. Muñoz, 1992). The initiation of the collisional stage at ca. 80 Ma was accompanied by the tectonic inversion of Early Cretaceous extensional basins. Following the slowing of the European/Iberian plate convergence at ~65 Ma (Roest and Srivastava, 1991), thrust activity resumed at 50 Ma. At 35–30 Ma, the exhumation rates accelerated to 2–4 km/Ma, in response to increasing thickening of the Iberian crust through underplating in the central Pyrenees (Fitzgerald et al., 1999) eventually enhanced by the Eo-Oligocene global cooling (Huyghe et al., 2009). Between the Late Cretaceous and the Eocene, the Iberian Plate followed a convergent motion relative to the European Plate, the rotation pole being located southwest of Iberia and consequently the compressional motion increased eastwards (Olivet, 1996). Later, compression decreased (Gorini et al., 1993). After the collision or during the last phase of plate convergence, the eastern Pyrenees (Fig. 1) were affected by a period of crustal thinning related to the well-defined Oligocene–Early Miocene rifting seen in the Gulf of Lions (Mauffret et al., 2001) that preceded the formation of the Western Mediterranean Sea (Réhault et al., 1984; Gorini et al., 1993). According to Mauffret et al. (2001), a second extensional event took place between the Late Miocene and the Early Pliocene. These authors suggest that prominent tectonic activity occurred during the Late Miocene, with most of the faults formed during this interval being sealed by the Messinian Erosional Surface. However, these authors consider that some extensional activity apparently persisted into the Early Pliocene but not later. Other authors (e.g. Briaies et al., 1990) assume that extension in the eastern Pyrenees continued during the Quaternary including the present day.

The eastern Pyrenees include two sedimentary basins infilled by Neogene sediments containing abundant pollen (Fig. 1B, C): (1) the uplifted Cerdanya Basin which today reaches an altitude of 1000 to

1200 m, bordered by high peaks up to ca. 2900 m a.s.l. This basin is characterised by two successive pollen floral assemblages, at Sanavastre and Sampor (Bessedik, 1985; Suc, 1989) and Can Vilella (Agustí et al., 2006; Fauquette et al., 2006), respectively of Tortonian and Messinian age (i.e. Upper Miocene) (Fig. 2); (2) the Roussillon coastal Zanclean Basin at the foot of the Canigou Mount, reaching an altitude of 2784 m (Fig. 2).

Uplift of the Cerdanya Basin was proposed by Mauffret et al. (2001) as having occurred mainly during the Middle to Late Miocene (between 10 and 5 Ma). During the 1990s, an intense debate arose concerning the tectonic activity in the eastern Pyrenees that took the form of destructive earthquakes in the area (for instance at Olot in 1427–1428; Olivera et al., 2008). For some authors, the associated normal faults indicate important tectonic activity during the Quaternary (Briaies et al., 1990).

Uplift of the Canigou Mount (Fig. 1B, C) occurred during the Late Miocene–Early Pliocene, as a result of a flexural isostatic rebound caused by crustal thinning. Based on the study of apatite fission tracks, Maurel et al. (2002) proposed that the onset of the exhumation of the Canigou Massif took place at around 27–26 Ma (Oligocene–Miocene). According to these authors, a second and last uplift pulse of the Canigou Mount occurred during the Messinian Salinity Crisis in the latest Miocene.

2.1. The Cerdanya Basin

The Cerdanya Basin is a SW–NE orientated half-graben (Fig. 1B, C) impacted by two tectonic phases (Pous et al., 1986; Cabrera et al., 1988; Roca, 1996): (1) during the Middle–Late Miocene, an intense fracturing of the eastern Pyrenees basement occurred, resulting in the dextral slip of the deep Têt Fault which formed the Cerdanya Basin; (2) in the latest Miocene (Messinian), the sedimentation terminated under a generally extensional situation. Neogene sediments, mostly consisting of fluvial sands and conglomerates, are 400 to 1000 m thick as a consequence of an intense subsidence (Agustí and Roca, 1987; Roca, 1996). These sediments consist of two units separated by an unconformity the lower unit being folded during an intervening phase (Cabrera et al., 1988). However, they contain diatomite, clay and lignite layers rich in mammal, ostracod and plant remains (including pollen).

Fossil mammals from the Sanavastre and Prats–Sampor localities (Cerdanya Lower Unit) belong to the Vallesian continental period (mammal zones MN 9–10). This is based particularly on the presence of *Hipparion primigenium catalaunicum* (Agustí and Roca, 1987), i.e. to the ca. 11–9 Ma interval (equivalent in part to the Tortonian Stage) (Fig. 2; Agustí et al., 2001).

The Can Vilella section exposes part of the Upper Unit. It contains small mammal teeth and bones which indicate that this Turolian fauna is of early Messinian age, based on palaeomagnetic measurements. It can be correlated to date from Chrons C3An.2n or C3An.1n for the topmost section (Fig. 2; Agustí et al., 2006). Whilst these authors argued in favour of a Chron C3An.1n date some doubt still remains. A revised biochronology of the Iberocitanian mammal faunas supports the younger date which is Chron C3An.1n (Gómez Cano et al., 2011). Nevertheless, the present authors consider this pollen flora was deposited between ca. 7 and 6 Ma, with the opportunity to test the two possible ages, close to 6.5 or 6.1 Ma, respectively.

Agustí et al. (2006) proposed that the elevation of Cerdanya reached at least 500 m during the Tortonian and over 1000 m in the late Messinian, considering that the difference in altitude between the Cerdanya Basin and the bounding high massifs to the north and south was already of the same order as that today, i.e. up to 1900 m (Fig. 1C). However, this assumption differs from that of Briaies et al. (1990), Coney et al. (1996) and Fitzgerald et al. (1999) who consider that the contrasting topography of the southern flank of the Pyrenees arose from erosion during the Messinian sea-level fall, rather than uplift.

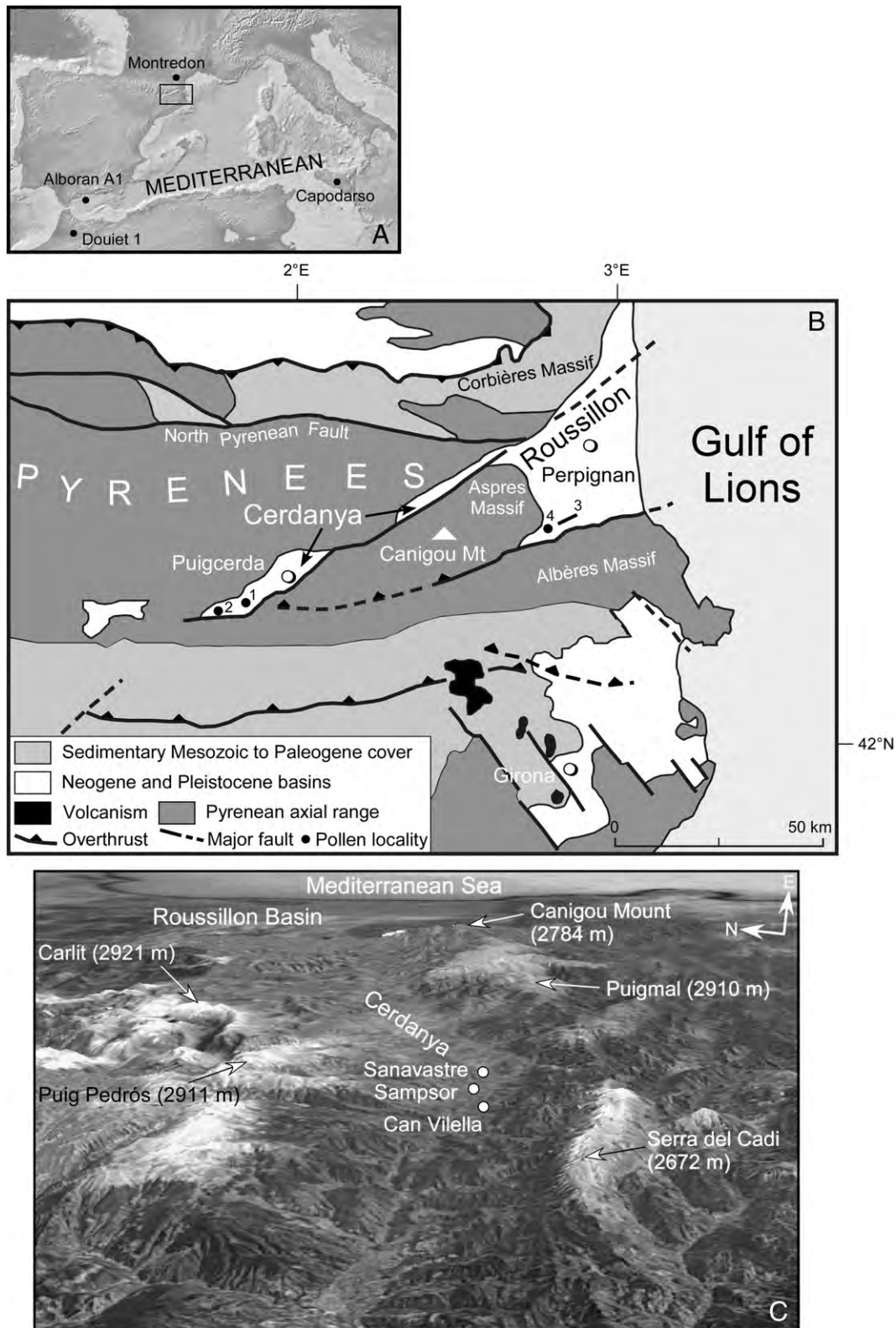


Fig. 1. Geography, geology and topography of the eastern Pyrenees. A, Location map of the studied area showing the pollen localities considered for this climatic comparison. B, Regional geological structure (from Briaies et al., 1990). Pollen localities: 1, Sanavastre and Sampsor; 2, Can Vilella; 3, Le Boulou; 4, Vivès. C, Three dimensional Google Earth view showing the Cerdanya and Roussillon basins and their bordering high massifs. The distance between the foreground and Mediterranean coastline is ca. 120 km.

2.2. The Roussillon Basin

The Roussillon Basin is a Neogene graben that was initially infilled by ca. 2000 m of Miocene deposits, then deeply eroded during the desiccation phase of the Messinian Salinity Crisis (Clauzon, 1990).

Zanclean coastal marine sediments, deposited within three deep coalescing rias, resulting from the Messinian fluvial canyons that were filled by sea when the Mediterranean Basin was reflooded (Clauzon et al., 1990; Bache et al., 2011). The Roussillon Basin is bordered to the west and south by the Pyrenees (the Aspès and Albères massifs,

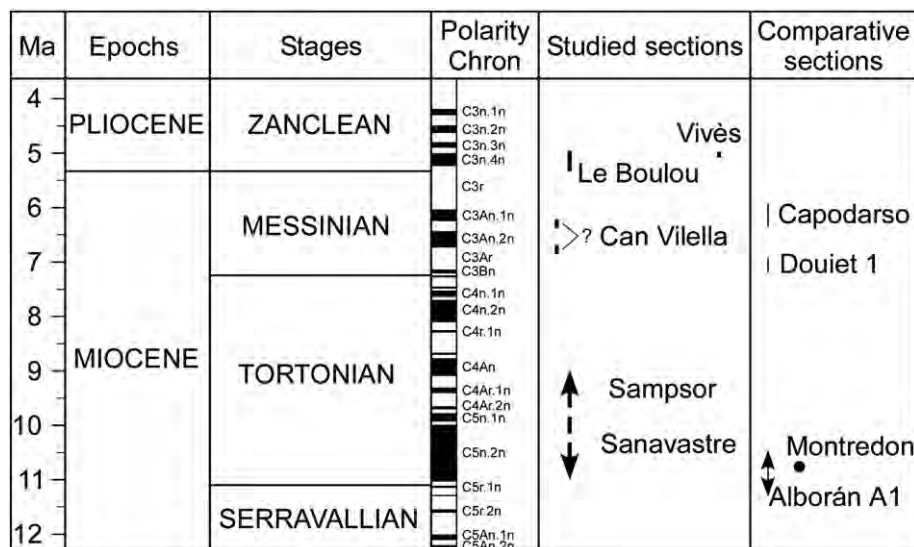


Fig. 2. Estimated chronostratigraphical position of the pollen floras studied and of the comparative pollen floras used for the palaeoaltitude reconstructions.

respectively), the Canigou Mount, composed of Hercynian rocks, reaching 2784 m only 49 km from the shoreline (Fig. 1B, C).

The basin contains abundant well-dated Zanclean pollen localities (Suc, 1976; Cravatte et al., 1984; Suc, 1989; Suc et al., 1992). Two localities, Le Boulou and Vivès, very close to the Canigou Mount (at 31 and 26.5 km, respectively), have provided rich pollen floral assemblages which are good candidates for estimating the altitude of the Canigou Mount in the early Zanclean (Fig. 2). Unfortunately, there is no Miocene pollen locality in the basin to provide an older pollen assemblage for comparison.

The Le Boulou section exposes clays (79 m thick) representing the prograding bottomset beds of a Zanclean Gilbert-type fan delta (Clauzon, 1990). This accumulation was dated using planktonic foraminifers from the Elne 1 and Canet 1 boreholes (Cravatte et al., 1984), and include the C3n.4n normal Chron (Fig. 2; Clauzon et al., 1990). The Vivès section includes thin lignite beds immediately overlying the prograding foreset beds and forming the marine–continental transition of the same Gilbert-type fan delta in its proximal part (Clauzon, 1990). These beds have yielded a rodent faunal assemblage (locality Vivès 2) which is of earliest Zanclean age (Fig. 2; Aguilar and Michaux, 1987; Clauzon et al., 1990).

3. Late Neogene vegetation in the eastern Pyrenees

3.1. Early Tortonian vegetation in Cerdanya

On the basis of the Sanavastre (42°23'N–1°51'E; Fig. 1B, C) and Sampsor (42°22'50"N–1°49'50"E; Fig. 1B, C) plant macro-remain and pollen localities (Figs. 1B, C, 3A, C), the early Tortonian Cerdanya lake was bordered by swamps that supported a luxuriant riparian forest (Martín-Closas, 1995). This is indicated by a diverse macroflora (*Glyptostrobus europaeus*, *Zelkova ungeri*, *Ulmus braunii*, *Taxodium distichum miocenicum*, several *Alnus*, *Salix* and *Populus* species, *Carya bilineata*, *Pterocarya denticulata*, *Myrica salicina* and *M. vindobonensis*, *Parrotia pristina* and *P. gracilis*, etc.: Menéndez Amor, 1955) and microflora (*Alnus*, *Carya*, *Liquidambar*, *Myrica*, *Nyssa*, *Parrotia persica*, *Pterocarya*, *Populus*, *Salix*, *Taxodiaceae* including *Taxodium*-type, *Ulmus*, *Zelkova*: Bessedik, 1985). Water plants colonised the most humid areas and/or marshes (macroflora: *Typha latissima*, *Trapa ceretana*, *Poaceae* p.p., *Cyperaceae*; Menéndez Amor, 1955; microflora: *Haloragis*, *Nymphaeaceae*, *Oenotheraceae*, *Potamogeton*, *Restionaceae*, *Sparganium*, *Typha*, *Poaceae* p.p., *Cyperaceae*; Bessedik, 1985).

As Menéndez Amor (1955) points out, the Cerdanya flora probably grew at a significantly lower altitude than that of the area today based on the abundance of evergreen mega-mesothermic (i.e. subtropical) plants: *Taxodiaceae* (*Taxodium*, *Glyptostrobus*), *Lauraceae* (*Laurus princeps*, *Cinnamomum lanceolatum*, *Sassafras ferretianum*, *Persea braunii*, *P. spinosa*), *Araucariaceae* (*Doliosirobium rerollei*), *Moraceae* (*Ficus tiliacifolia*, *F. pulcherrima*), *Proteaceae* (*Embothrium microsporum*, *Dryandroides* aff. *banksioefolia*, *D. lignitum*, *Banksia deikeana*, *B. helvetica*, *Conospermum macrophyllum*), *Fabaceae* *Caesalpinoideae* (*Caesalpinia* cf. *lepidia*, *C. townshendi*, *C. micromera*, *Cassia paleogea*, *C. ambigua*, *C. lignitum*, *C. berenices*), *Sapindaceae* (*Sapindus dubius*), *Celastraceae* (*Celastrus crassifolius*), *Sapotaceae* (*Sapotacites minor*, *S. parvifolius*), etc. This aspect is supported by pollen flora (Bessedik, 1985) with *Cassia* (*Fabaceae* *Caesalpinoideae*), *Celastraceae*, *Distylium* (*Hamamelidaceae*), *Engelhardia* and *Platycarya* (*Juglandaceae*), *Nyssa* cf. *sinensis* (*Nyssaceae*), *Sapotaceae*, and *Taxodiaceae* (Fig. 3B, D).

Development of vegetation belts above those mentioned is demonstrated by Menéndez Amor (1955) by successively (1) deciduous mesothermic (i.e. warm–temperate) plants (*Acer*, *Juglans*, many *Quercus* species, *Carpinus*, *Ostrya*, *Betula*, *Tilia*, *Platanus*, *Castanea*, *Buxus sempervirens*, etc.), (2) deciduous meso–microthermic (i.e. cool–temperate) plants (*Fagus pliocenica* var. *ceretana*, *F. pristina*, *F. cf. castanaefolia*), and (3) evergreen conifers (*Pinus*, *Abies saportana*). Such an altitudinal organisation is also clear when considering the pollen flora (Bessedik, 1985; see the Method for estimating palaeoaltitude of an uplifted basin section for further explanation): (1) a deciduous mesothermic assemblage (*Acer*, *Buxus sempervirens*, *Carpinus*, *Celtis*, *Juglans*, *Ostrya*, *Platanus*, *Quercus*), (2) a mixed meso–microthermic assemblage (*Fagus* and *Cathaya* mainly, *Tsuga*), and (3) a coniferous microthermic assemblage (*Pinus* p.p., *Abies*) (Fig. 3B, D).

Palaeoclimatic parameters have been determined for the lowermost vegetation belt of Cerdanya using the 'Climatic Amplitude' transfer function for pollen records (Fauquette et al., 1998): the mean annual temperature (MAT) was between 15.5 °C and 19.8 °C with a 'Most Likely Value' (MLV) of 17.4 °C (Table 1), the annual precipitation was between 1100 and 1600 mm with a MLV at 1300 mm (Fauquette et al., 2007; Jiménez-Moreno et al., 2010).

To summarise, these data indicate that the Cerdanya Basin was significantly lower in altitude during the early Tortonian than today because it supported a rich mega–mesothermic flora. Indeed, the present-day flora mostly comprises mesothermic and meso–microthermic elements (*Quercus pubescens*, *Acer*, *Corylus*, *Betula*, etc.; Gaussen, 1972; Gaussen et al., 1972). In addition, the surrounding massifs were already relatively

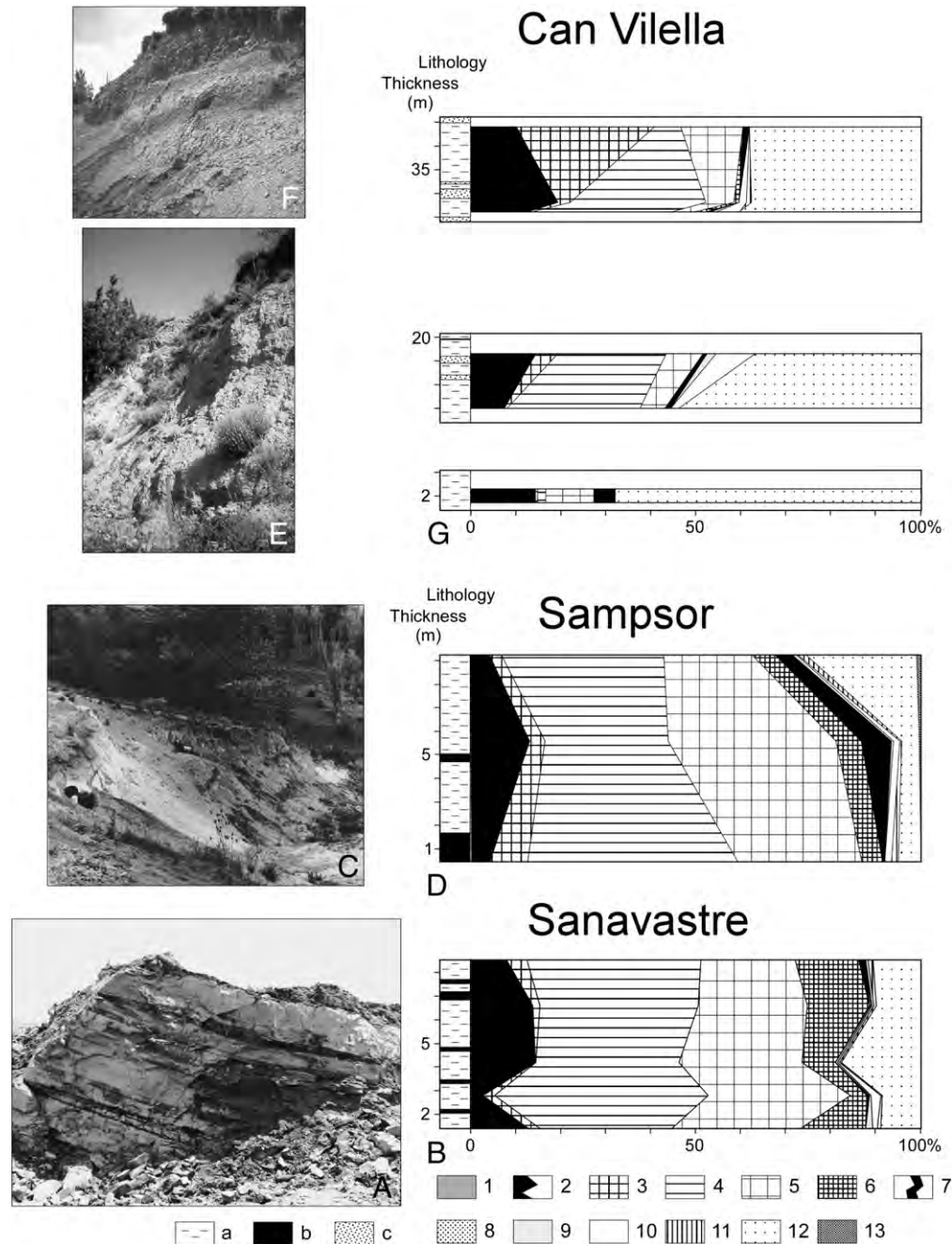


Fig. 3. Pollen localities from Cerdanya. Sanavastre: A, View of the sampled section. B, Synthetic pollen diagram. Sampsor: C, View of the sampled section. D, Synthetic pollen diagram. Can Vilella: E, View of the middle part of the section. F, View of the upper part of the section. G, Synthetic pollen diagram of the section in three segments, respectively located at the base, in the middle part and upper part of the section (for details, see: Agustí et al., 2006). Lithology: a, clay or diatomite; b, lignite; c, gravels. Ecological pollen groups according to Nix (1982) for their present thermal classification: 1, megathermic elements ($\text{MAT} > 24^\circ\text{C}$); 2, mega-mesothermic elements ($20^\circ\text{C} < \text{MAT} < 24^\circ\text{C}$); 3, *Cathaya*, a conifer restricted today to the Chinese mixed deciduous forest (cf. Fig. 7); 4, mesothermic elements ($14^\circ\text{C} < \text{MAT} < 20^\circ\text{C}$); 5, *Pinus*; 6, meso-microthermic elements ($12^\circ\text{C} < \text{MAT} < 14^\circ\text{C}$); 7, microthermic elements ($\text{MAT} < 12^\circ\text{C}$); 8, Cupressaceae composed of elements living under various conditions; 9, elements which cannot be used because of the insufficient level of pollen identification or their ecological ubiquity; 10, hygrophilous plants; 11, Mediterranean xerophytes; 12, herbs; 13, steppe elements.

high according to the critical elevated frequency of meso-microthermic and microthermic elements, especially in the pollen record. A slight cooling seems to have characterised the Sampsor pollen flora by comparison with that of Sanavastre, resulting in a larger representation of *Abies* (Fig. 3D) probably caused by some descent of the most elevated forest belt.

3.2. Early Messinian vegetation in Cerdanya

The early Messinian vegetation of Cerdanya is only documented by pollen data from the Can Vilella locality ($42^\circ20'50''\text{N}$ – $1^\circ47'\text{E}$;

Figs. 1B, C, 3E, F) (Agustí et al., 2006). Cooler conditions than during the Tortonian characterise the Can Vilella flora since it contains only a few mega-mesothermic elements (Cyrillaceae–Clethraceae, *Engelhardia*, *Leea*, *Nyssa*, Sapotaceae and Taxodiaceae) with a predominance of Taxodiaceae and, at a lesser extent, *Engelhardia* (Fig. 3G). This could result from tectonic uplift of the area because no major cooling occurred within the time interval 10–6 Ma (Zachos et al., 2001; Westerhold et al., 2005). Early Messinian riparian forests were dominated by *Alnus*, *Carya*, *Pterocarya*, *Salix*, *Ulmus*, *Zelkova*, and above all Taxodiaceae, all of which maintained swampy and marshy (according to the high frequency of Cyperaceae and Poaceae *p.p.*)

Table 1
Latitude–palaeolatitude and mean annual temperature (MAT) values used for estimating the palaeoelevation of the Cerdanya Basin during the Late Miocene. MLV, Mean Likely Value.

Locality			North latitude	Difference in latitude with locality 1 or 4 (DI)	Difference in palaeolatitude with locality 1 or 4 (DI)	MAT (°C) = t ₁ or t ₂			t ₃ (°C) MLV	Palaeoelevation (Pe) (m)
						Min.	MLV	Max.		
Early Messinian	6	Capodarso	37°33′	4°47′50″	35°	15.6	22.5	24.7	20.4	600
	5	Douiet 1	34°2′25″	8°18′25″	8.7°	21.6	23.6	24.7	18.4	250
	4	Can Vilella	42°20′50″			15.5	17	19.8		
Early Tortonian	3	Montredon	43°11′	48′	0.74°	15	17	22	17.4	Near sea level
	2	Alborán A1	36°38′	5°45′	4°	17	20.3	25	17.9	100
	1	Sanavastre–Sampsor	42°23′			15.5	17.4	19.8		

environments. A similar altitudinal organisation of the vegetation persisted (see the [Method for estimating palaeoaltitude of an uplifted basin](#) section for further explanation) with a more pronounced opening of forests according to the large frequency of herbs ([Fig. 3G](#)). Nearby high summits existed based on the occurrence of *Abies* and *Picea*.

As previously mentioned, palaeoclimatic parameters have been calculated: MAT was between 15.5 °C and 19.8 °C with MLV at 17 °C ([Table 1](#)), the annual precipitation lay between 1070 and 1300 mm with MLV at 1100 mm ([Fauquette et al., 2006](#)).

3.3. Early Zanclean vegetation in the Roussillon Basin

Two pollen localities, Le Boulou (from 42°31′24″N–2°50′38″E to 42°32′29″N–2°52′E; [Fig. 1B](#)) and Vivès (42°31′36″N–2°47′E; [Fig. 1B](#)), yield evidence for the vegetation of the Roussillon Basin and the eastern slope of the Canigou Mount during the early Zanclean ([Figs. 4 and 5](#)). These localities are very close to the Canigou Mount as can be seen in [Fig. 5C](#). Taxodiaceae swamps (with *Nyssa*) and marshes (with Cyperaceae, *Myrica*, Cyrellaceae–Clethraceae, Poaceae and water plants such as *Typha*, *Potamogeton*, *Euphorbia* cf. *palustris*) occupied the coastal sites. The lowlands were inhabited by a subtropical forest composed of evergreen and deciduous trees, such as Sapotaceae, Hamamelidaceae (*Hamamelis*, *Distylium*), Celastraceae, Menispermaceae, Taxodiaceae, Arecaceae, Juglandaceae (*Engelhardia*) and Fagaceae (*Quercus*). Rivers were bordered by a riparian forest with *Alnus*, *Salix*, *Populus*, *Pterocarya*, *Liquidambar*, *Ulmus*, *Zelkova*, *Parrotia persica* and *Platanus*, etc. Evergreen sclerophyllous elements lived in drier places (Mediterranean xerophytes: *Olea*, *Phillyrea*, *Pistacia*; *Microtropis fallax* and *Pinus p.p.*). The lower slopes of the Canigou Mount supported deciduous forest (*Quercus*, *Carya*, *Carpinus*, *Acer*, *Tilia*, *Betula*, etc.), successively replaced at higher altitudes by a mixed forest (with *Fagus*, *Cedrus*, *Cathaya*, *Sciadopitys*, *Tsuga* and *Pinus p.p.*) and a coniferous forest (*Abies*, *Picea*, *Pinus p.p.*) (see the [Method for estimating palaeoaltitude of an uplifted basin](#) section for further explanation). Accordingly, the altitude of Canigou Mount was already high at that time.

Following the same method as for the Late Miocene, palaeoclimatic parameters have been determined: MAT was between 14.6 °C and 17.7 °C with MLV at 16.5 °C, the annual precipitation was between 1180 and 1270 mm with a MLV at 1200 mm ([Fauquette et al., 2007](#)).

4. Method for estimating palaeoaltitude of an uplifted basin

Tectonic motion of uplifted basins requires quantification over long periods, if possible supported by multiple approaches. [Axelrod \(1997\)](#) devised a method based on the estimated difference in temperature between a palaeoflora from an uplifted locality and a similar modern flora living in lowlands. The present authors have developed a different method, based on the same concept but using almost coeval Neogene pollen floras (*i.e.* located in the same chronological

range as the pollen flora studied: see [Fig. 2](#) and text below), which benefits from several advantages:

- lowland pollen localities selected for comparison are relatively frequent since they are coastal marine sediments which are often accurately dated,
- thermal latitudinal and altitudinal gradients established by [Ozenda \(1989\)](#) allow a standardised application,
- quantification of the latitudinal thermal gradient for the Neogene of Europe ([Fauquette et al., 2007](#)) allows the use of the modern values for the period since the earliest Tortonian.

The method perfected for this purpose is as follows ([Fig. 6](#)):

- as mentioned above, the MAT is calculated for the uplifted pollen locality at the time of deposition, this is the value t₁;
- MAT is also calculated for a contemporaneous stable pollen locality in the lowlands, this is the value t₂;
- the present-day difference in latitude (DI) between the two localities is measured, possibly replaced by the palaeodifference obtained from palinspastic reconstructions for the studied time;
- MAT t₂ is translated into t₃ using the difference in latitude (or palaeolatitude) between the two localities with respect to the latitudinal thermal gradient (or palaeogradient) (Lgr expressed in °C per degree of latitude) using the equation: t₃ = t₂ + (DI × Lgr); MLV of t₃ is considered as MAT of the pollen locality if it was not uplifted;
- palaeoelevation (Pe expressed in hundred metres) of the pollen locality at the time of sediment deposition is obtained using the difference in MLV of t₃ and t₁ and applying the altitudinal thermic gradient (or palaeogradient) (Agr expressed in °C per hundred metres) according to the equation: Pe = (t₃ – t₁) / Agr.

This method has been tested to estimate the palaeoaltitude of the Cerdanya Basin during the early Tortonian (11–9 Ma) and early Messinian (7–6 Ma) times. The authors used the same modern thermal gradient as that of [Fauquette et al. \(2007\)](#) who established that the shift from a latitudinal thermal gradient at 0.48 °C per degree of latitude to the modern one (0.6 °C per degree of latitude) was already achieved at 11 Ma.

The palaeoaltitude estimates were calculated using the MLVs of MAT obtained from pollen data. The MLVs are certainly less representative of the climate than the entire reconstructed climatic amplitude (as plants may sometimes support large climatic ranges), however they provide a good idea of the optimum climate where they best develop. Moreover MLVs have been statistically tested on modern pollen data and, as a consequence, they are considered to give reliable results ([Fauquette et al., 1998](#)).

A validation of the method may be achieved using a modern pollen flora sampled at Col de Jau (42°41′N–2°15′E; cf.: Supplementary data 1 and 2) using a method developed by [Cour \(1974\)](#). This consists of whipping up dust (including pollen grains) and collecting it on filters, using a car travelling along several two-way journeys on a pathway

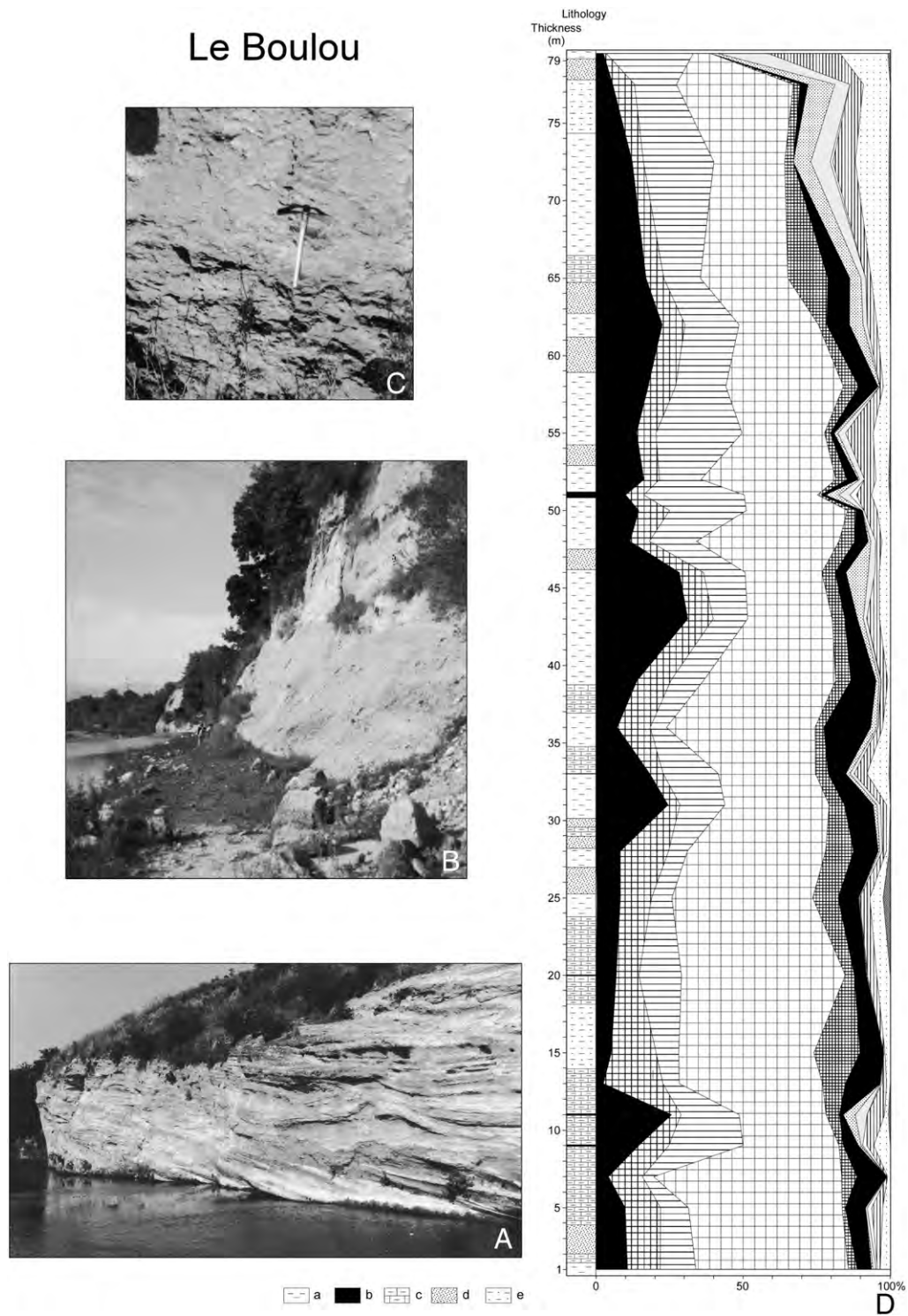


Fig. 4. Pollen locality of the Le Boulou sequence (Roussillon Basin). A, View of the lowermost part of the section. B, View of the middle part of the section. C, View of the uppermost part of the section. D, Synthetic pollen diagram of the section. Lithology: a, grey clays; b, lignite; c, whitish marls; d, sands and gravels; e, grey silts. Ecological pollen groups: same caption for Fig. 3.

(1 km long at constant altitudinal level). Simultaneously, a plant inventory of the area is obtained in order to determine which pollen grains are of local origin and which are not. The climatic reconstruction from the Col de Jau pollen flora indicates a MAT between 3 and 12 °C with MLV around 7.5 °C. This value is found today for example at around 58°N in Norway, *i.e.* 15° further north than the Col de Jau locality. Using the relation established by Ozenda (1975, 1989), this difference in latitude indicates an estimated altitude of the sampled site of

~1650 m a.s.l. Actually, Col de Jau occurs today at 1506 m a.s.l. In the same way, the climatic reconstruction determined from a modern pollen flora sampled at Canet–Saint-Nazaire, at sea level (42°40'N–3°00'E; *cf.*: Supplementary data 1 and 2) indicates MAT between 9.5 and 24.7 °C with an MLV around 16.7 °C. Using the same approach as that used for the fossil pollen data, comparing the two modern sites which occur at the same latitude, a difference of MAT of 9.2 °C indicates a reconstructed altitude of about 1670 m for Col de Jau. These results indicate that,

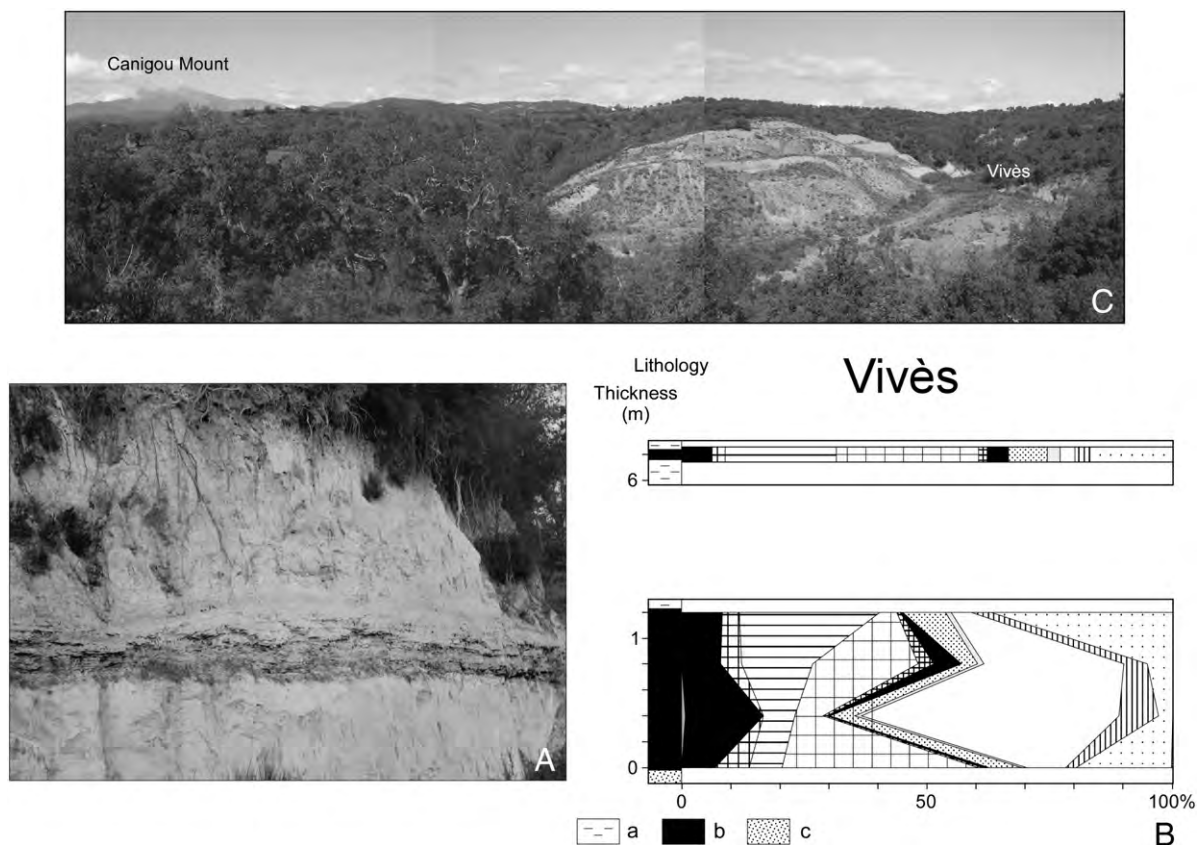
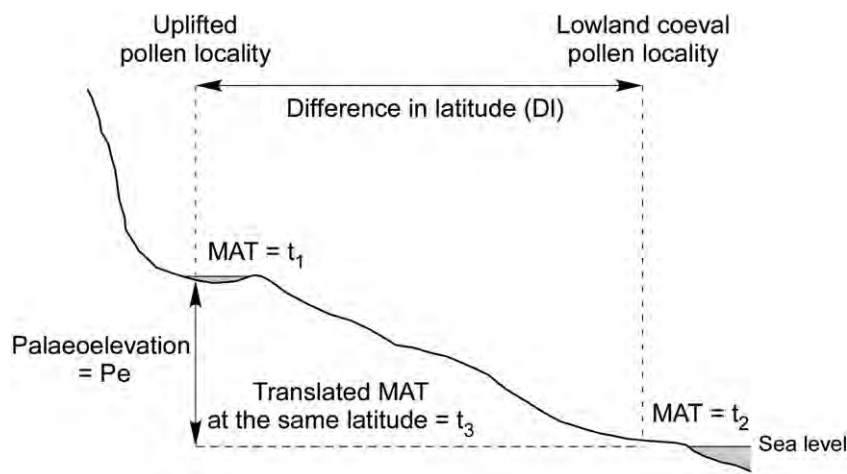


Fig. 5. Pollen locality of Vivès (Roussillon Basin). A, View of the section. B, Synthetic pollen diagram of the section in two segments, respectively located in the middle part and uppermost part of the section. Lithology: a, grey clays; b, lignite; c, sands and gravels. Ecological pollen groups: same legend as Fig. 3. C, Panorama showing the short distance from the Canigou Mount to the Vivès section.

although the reconstructed climatic interval is large, the MLV gives a reliable estimate for the site's altitude at the time of deposition.

For a large part, the reconstructed altitudinal vegetation depends on the assumption that the Neogene plants occurred in the same altitudinal vegetation belts (Fig. 7) as those today, as assumed above. This consideration of two altitudinal vegetation belts (a *Cathaya–Tsuga–Cedrus* belt succeeded by an *Abies–Picea* belt) results from interpretation of a large set of data established over a long time period (Suc, 1989; Suc et al., 1999):

- pollen floras (coastal marine and lowland lacustrine localities) from the four best-documented Neogene stages (Burdigalian, Langhian, Messinian, Zanclean) show enrichment in *Cathaya* and *Tsuga* (and often *Cedrus*) near old (or lower) massifs. They also show an enrichment in *Abies* and *Picea* near recent (higher) massifs (Bessedik, 1985; Suc, 1989; Suc et al., 1995a, 1995b, 1999; Popescu, 2001, 2006; Jiménez-Moreno, 2005; Fauquette et al., 2006; Popescu et al., 2006, 2010; Jiménez-Moreno and Suc, 2007; Jiménez-Moreno et al., 2007b, 2010);



MAT = mean annual temperature

Fig. 6. Method for estimating the palaeoaltitude of an uplifted basin with the associated parameters.

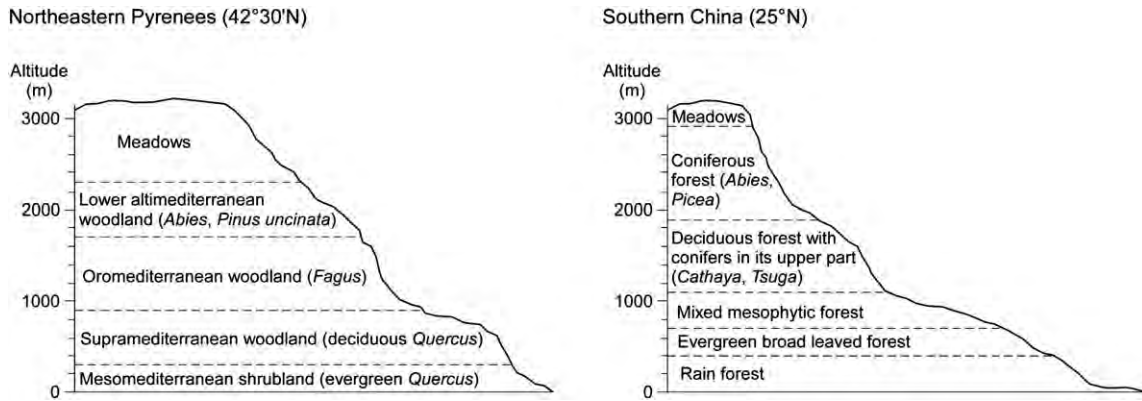


Fig. 7. Present-day schematic altitudinal organisation of vegetation in the northeastern Pyrenees (latitude 42°30'N; Gruber, 1980), based on vegetation belts defined by Ozenda (1975) compared with that in southern China (latitude 25°N; Wang, 1961).

- concerning the Alps, these pollen floral assemblages show enrichment in *Cathaya* (Aquitainian–Burdigalian) prior to that in *Abies* and *Picea* (Langhian to Zanclean). This is interpreted as reflecting increasing elevation of the chain (Suc et al., 1992; Jiménez-Moreno et al., 2005, 2008);
- the spatial distribution of plants, with respect to their latitudinal replacement at a given moment, is consistent with the proposed altitudinal arrangement (Fauquette et al., 2007);
- palaeovegetation maps obtained from interpolated pollen data (Favre, 2007) or from palaeoclimate modelling (François et al., 2011), also support this vegetational organisation.

These conclusions confirm the present vegetation of China as the best model for the organisation of Neogene vegetation in southern Europe (Fig. 7).

At first sight, the method applied herein could possibly appear to be biased by variations in temperature relative to astronomical cycles, for example if two pollen floras from the same chronological interval indicating different temperature are compared. During the warm Miocene and Pliocene interval, variability in MAT did not usually exceed 2 °C in the Mediterranean region (Fauquette and Bertini, 2003; Jiménez-Moreno et al., 2005, 2007a; Fauquette et al., 2006), whereas it was significantly more important during the Quaternary (>6 °C; Fauquette and Bertini, 2003; Klotz et al., 2006). Accordingly, such a variability of ± 1 °C for the Neogene could be neglected because the method is designed to provide a rough guide to palaeoaltitude rather than its precise value. In addition, when several varying pollen spectra are obtained from a locality, they can be grouped when an MAT representative of the whole time-span of the sediments is determined. This is the case for the Sanavastre, Sampsor and Can Vilella sequences and their comparative pollen floras from Alboran A1, Montredon, Douiet 1, Capodarso, respectively. In this way, the potential variability in temperature has been integrated into the calculations.

5. Early Tortonian and early Messinian palaeoaltitude of the Cerdanya Basin

5.1. During the early Tortonian (11–9 Ma)

The pollen assemblage of marine sediments at 1073–1129 m depth from the offshore Alborán A1 borehole (Alboran Sea: 36°38' N–4°13'23"E; Fig. 1A) is the closest site contemporaneous with the Sanavastre–Sampsor pollen floras. The well-dated (by planktonic foraminifers) Tortonian marine sediments from the Alborán A1 borehole (Fig. 2) provided a pollen assemblage dominated by herbs representative of the nearby coastal lowlands at the time of closure of the Betic Corridor. They also occurred before significant elevation of the Betic Ranges (Krijgsman, 2002) documented by low abundance of

Cathaya (Jiménez-Moreno, 2005; Fauquette et al., 2007; Jiménez-Moreno et al., 2010). The MAT range for this pollen flora (t_2) is 17–25 °C with an MLV of 20.3 °C (Jiménez-Moreno et al., 2010). Today, the difference in latitude between these two localities is 5°45'. However it can be reduced to 4° (DI) if palinspastic reconstructions for the Serravallian–Tortonian times are reconsidered (Meulenkamp and Sissingh, 2003; Paramonova et al., 2004). In this case the translated MLV t_3 (using Lgr at 0.6 °C per degree of latitude; Fauquette et al., 2007) equals 17.9 °C. Considering an Agr value at 0.55 °C per 100 m (Fauquette et al., 2007), this gives a palaeoelevation (Pe) of ca. 100 m based on the MLV (Table 1) bearing in mind that the climatic ranges are large.

Similarly, we compared the Sanavastre–Sampsor pollen floras with that from the early Tortonian-age levels of the Montredon locality in southern France (43°11'N–2°55'E; Fig. 1A). At Montredon, lacustrine sediments (dated by mammal zonation: Aguilar et al., 2004; Fig. 2) provided a pollen assemblage derived from the North Pyrenean lowlands. It includes an indication of moderate relief by the presence of *Cathaya* pollen (Bessedik, 1985). The Montredon MAT range is 15–22 °C with an MLV at 17 °C. Today, the difference in latitude between the two localities is 48' (i.e. 0.80°), but can be reduced to 0.74° based on palinspastic reconstructions (Meulenkamp and Sissingh, 2003; Paramonova et al., 2004). Here the MLV t_3 should equal 17.4 °C if Sanavastre–Sampsor was at sea level (Table 1). This suggests that the Cerdanya Basin occurred near the seashore at a very low palaeoaltitude at that time.

Such a low palaeoaltitude can be seen within the range of significance of the 'Climatic Amplitude' transfer function which concerns 'low/middle–low altitude vegetation', i.e. approximately the lowermost 200 m (Fauquette et al., 1998). Therefore, we consider a maximum elevation of 200 m a.s.l. for the Cerdanya Basin during the early Tortonian interval (Fig. 8), an option consistent with the palaeogeographic map published by Paramonova et al. (2004).

5.2. At the early Messinian (7–6 Ma)

Two pollen floras have been used for this estimation:

- the Douiet 1 borehole in Morocco (34°2'25"N–5°7'35"W; Fig. 1A) which yielded well-dated (by planktonic foraminifers) marine sediments (Fig. 2); its pollen assemblage, dominated by xeric herbs, originated from the nearby lowlands bordering the northern shoreline of the Rifan Corridor. Here deciduous *Quercus* is the sole indicator of some local relief (Bachiri Taoufiq et al., 2008);
- the Capodarso exposure in Sicily (37°33'N–14°9'E; Fig. 1A), the uppermost part of which exposes marine coastal sediments including Chron C3An.1n (Fig. 2; Suc et al., 1995c). The contained open xeric pollen assemblage derived from nearby lowlands at the foot of the Nebrodi–Madonie Mounts, the low elevation of

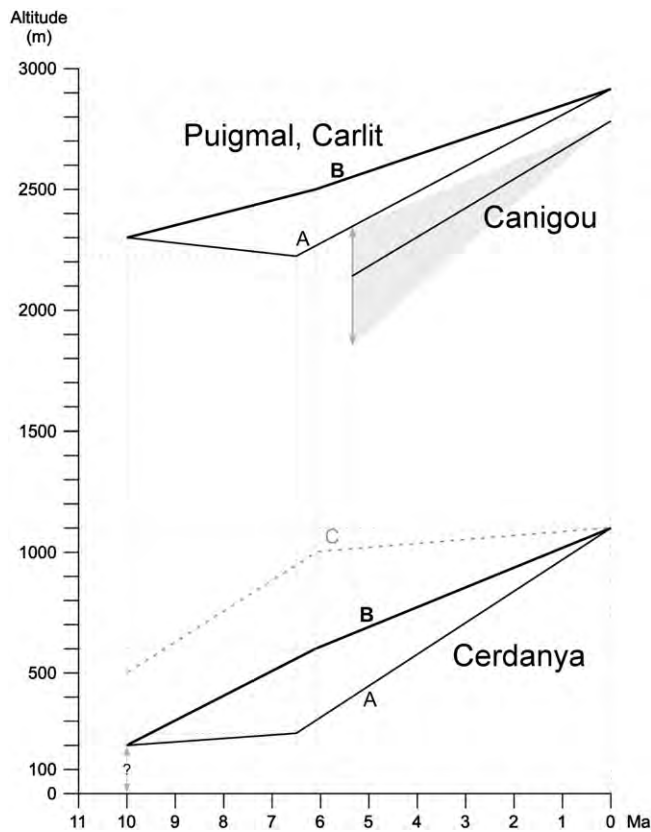


Fig. 8. Optional proposed uplift rates of the Cerdanya Basin, Puigmal and Carlit surrounding massifs, and Canigou Mount between 10 Ma (intermediate point between 11 and 9 Ma) compared to today. Uncertainty ranges are indicated by a double arrow. A, Option for 6.5 Ma for the top of the Can Vilella section; B, Preferred option for 6.1 Ma for the top of the Can Vilella section. C, Option proposed by Agustí et al. (2006), for 6.1 Ma for the top of the Can Vilella section.

which is indicated by the occurrence of deciduous *Quercus* and rare *Cathaya* pollen (Suc et al., 1995c).

The MAT values have been calculated for this sequence using the 'Climatic Amplitude' transfer function, and gave the following ranges (Fauquette et al., 2006):

- Douiet 1: 21.6–24.7 °C, MLV at 23.6 °C;
- Capodarso: 15.6–24.7 °C, MLV at 22.5 °C.

Applying the same calculation as previously for the MLV values, after taking into account difference in palaeolatitude, indicated by Khondkarian et al. (2004) (Table 1), an elevation of 250 m with respect to the Douiet 1 palaeotemperature and 600 m with respect to the Capodarso palaeotemperature was obtained (Table 1).

The present palaeoaltitude estimates for the Cerdanya Basin, though they are not sufficiently precise, offer an indication of a trend in its uplift progression since 10 Ma (Fig. 8). At that time, a maximum palaeoaltitude is suggested to be 200 m considering the imprecision arising from the 'Climatic Amplitude' transfer function (see above). From this, two options can be suggested (Fig. 8):

- option A, with an elevation of ca. 250 m at 6.5 Ma (just before the end of Chron C3An.2n); this option suggests an accelerated uplift rate since 6.5 Ma;
- option B, with an elevation of ca. 600 m at 6.1 Ma (just before the end of Chron C3An.1n); this option suggests an almost constant uplift rate from 10 Ma to the present.

In either case, these options differ significantly from option C proposed by Agustí et al. (2006), which suggested a marked decrease in the uplift rate since 6 Ma (Fig. 8).

6. Palaeoaltitude of the Canigou Mount in the early Zanclean

The early Zanclean pollen floras of the south Roussillon Basin (Figs. 4 and 5), described above, are rich in *Cathaya*, *Cedrus* and *Tsuga*, *Abies* and *Picea*. These results imply that a complete altitudinal forest succession occurred on the Canigou Massif when subtropical climatic conditions dominated on the coastal plain. This observation allows the application of the method developed by Fauquette et al. (1999) for estimating a minimum palaeoaltitude of the Canigou Mount. This method takes into account pollen assemblages accumulated near the coast that provides a regional view of the vegetation from the coastal beaches to the uppermost altitudinal belts.

Ozenda (1989) established that a shift of 1 km to the north is equivalent, from a bioclimatic point of view, to a shift of 1 m in altitude. Therefore, today, vegetation belts shift by a mean value of 110 m in altitude per degree in latitude. Applying this relationship, the vegetation distribution to the climatic estimates, it is possible to reconstruct the altitude of the Canigou Mount in the earliest Pliocene:

- at that time, the MAT at Le Boulou, situated at about 42.5°N latitude, was about 16.5 °C on the coast (range comprised between 14.6 and 17.7 °C) (Fauquette et al., 2007). Today, such a temperature occurs south of Valencia in Spain, at about 38.5°N latitude on the seashore, i.e. about 4° lower in latitude than Le Boulou (or between 1.5 and 6° lower in latitude if the range of reconstructed MAT is considered);
- using the relationship established by Ozenda (1975, 1989), a shift of 4° in latitude corresponds to a mean shift of about 440 m in altitude. Thus, in the earliest Pliocene, vegetation belts should be shifted about 440 m higher (or 165 to 660 m based on the MAT interval mentioned above);
- today, *Abies* may be established between ca. 900 (the lowest altitude of occurrence of individual *Abies* trees) and 2000 m high in the Canigou Massif. However, the lower altitudinal limit of fir forests in this massif can be estimated at an altitude ca. 1700 m (Fig. 7; Gausson et al., 1972; Gruber, 1980). Taking into account the shift of 440 m in vegetation belts between modern day and the earliest Pliocene, fir occurred from about 2140 m or 1865 to 2360 m, based on the climatic interval (Fig. 9). These values are an estimate of palaeoaltitude of the lower limit of the *Abies* belt. Therefore, they indicate only a minimum altitude for the Canigou Mount at the beginning of the Pliocene. It should have been at least 1865 m high above the sea level and more probably higher than 2140 m (Fig. 8).

7. The altitudinal difference between Cerdanya and the surrounding massifs

It is also possible to attempt to estimate the altitude of massifs surrounding the Cerdanya Basin in early Tortonian and early Messinian times. For this purpose, the MLV of MAT indicated by pollen assemblages of Sanavastre–Sampso and Can Vilella are used here (Table 1).

Applying a value of 0.55 °C per 100 m for the altitudinal thermal gradient (Agr) to the early Tortonian, it is possible to use the translated MLV of MAT value at sea level for the Sanavastre–Sampso pollen floras (t_3 calculated from Montredon and Alborán A1 localities in Table 1). In this case they would fall between 17.4 and 17.9 °C. The Sanavastre–Sampso pollen floras indicate a vegetation sequence capped by the *Abies* forest. The authors determine the latitudes where such values of MAT are recorded today. These latitudes are reported on the altitude versus latitude distribution of the *Abies* belt that allows to determine its basal altitude and hence a minimum altitude of the nearby Puigmal and Carlit massifs (today 2910 and

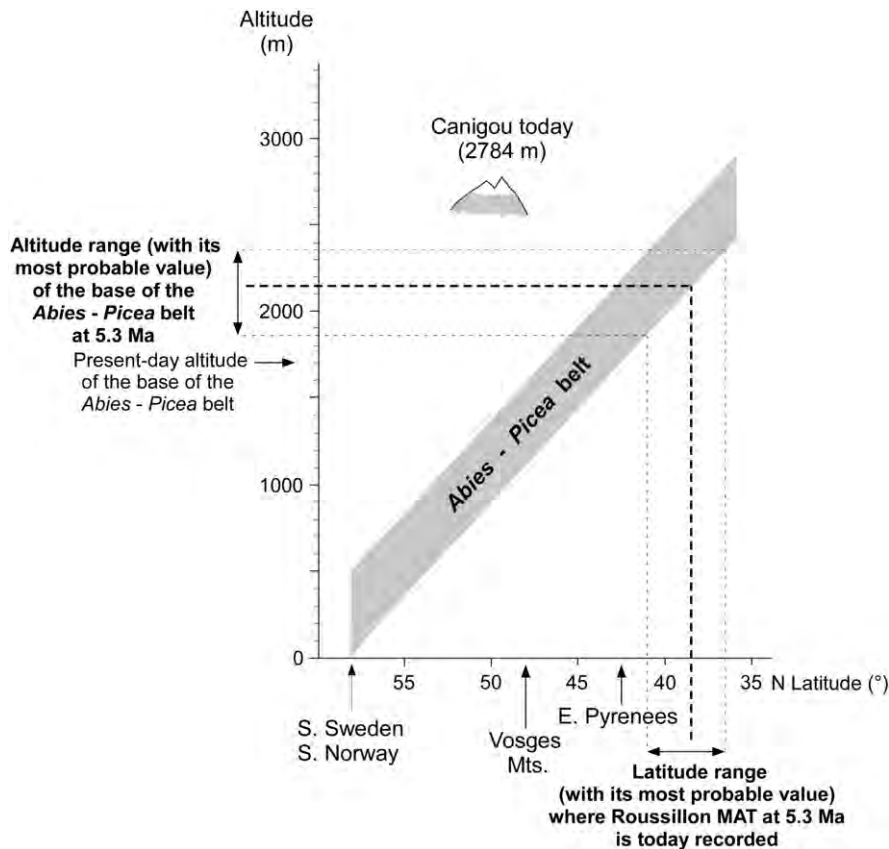


Fig. 9. Altitudinal range of the *Abies*–*Picea* belt according to latitude from northern to southern Europe (Ozenda, 1975, 1989). The horizontal bold dashed line: estimated altitude (with its confidence interval: normal horizontal dotted lines) of the base of this ultimate forest belt at the earliest Pliocene with respect to the mean annual temperature (MAT) reconstructed for the Roussillon Basin at that time (vertical bold dashed line: latitude where MLV is today measured; vertical normal dashed lines: latitudinal incertitude range according to incertitude on MAT). Comparison with the present-day altitude of the Canigou Mount.

2921 m, respectively; Fig. 1C). At present, these temperatures are recorded further to the south, at around 37° and 36.4°N, respectively. Adopting the relationship established by Ozenda (1975, 1989), 1° of latitude corresponds to 110 m in altitude, and the present-day lower altitudinal limit of *Abies* in these massifs (around 1700 m; Fig. 7; Gaussen et al., 1972; Gruber, 1980), the Puigmal and Carlit massifs should have been at least 2300 m high at 11–9 Ma (Fig. 8).

As the Can Vilella pollen flora demonstrates the *Abies* and *Picea* pollen evidences, the same calculation made for the early Tortonian can be performed for estimating palaeoaltitude of the Puigmal and Carlit massifs during the early Messinian. Here the two optional translated values of the MLV of MAT of the Can Vilella pollen flora at sea level of 18.4 °C and 20.4 °C (t_3 calculated from Douiet 1 and Capodarso localities in Table 1), correspond to 250 m or 600 m (options A and B in Fig. 8, respectively) of palaeoaltitude for the Cerdanya Basin. This results in two options for the minimum altitude of the nearby massifs. Today these temperatures are recorded further to the south, respectively around 37.5°N and around 35°N. Therefore, the Puigmal and Carlit massifs have been at least 2220 m high at 6.5 Ma (option A) or 2500 m high at 6.1 Ma (option B) (Fig. 8).

8. Discussion and concluding remarks

The considerable interest of this case study is the presence in a small area of three chronologically distinct plant records. On this basis, it is possible to emphasise some concepts that can be considered objectively as robust outcomes:

- the Cerdanya Basin was a low altitude area during the early Tortonian as indicated by the substantial diversity of mega-mesothermic

plants it sustained. Indeed it probably corresponds to the option proposed by Dèzes et al. (2004) in their reconstruction of the European Cenozoic rift system using several maps distributed through the time, even if the authors did not clearly express this assumption;

- Cerdanya was at that time surrounded by already significantly elevated massifs because its deposits contain frequent to abundant *Abies* pollen grains. This interpretation is supported by the rare occurrence of *Picea* pollen (a taxon able to withstand colder conditions than *Abies*; Noïrfalisse et al., 1987) in the Can Vilella younger pollen assemblage. This observation agrees with a probable uplift between 11–9 and ca. 6 Ma;
- the existence of an already elevated Canigou Mount in the earliest Pliocene, an observation based on the high frequency of *Abies* and *Picea* pollen in Le Boulou sequence.

Even if the numerical values obtained are questionable, a reconstructed uplift of the eastern Pyrenees since 10 Ma is proposed. In particular the preferred option B seems sufficiently realistic to initiate new questions or re-open previous discussions (Fig. 8). Indeed, this option, the chronology of which is supported by the clarified age of Can Vilella (Gómez Cano et al., 2011), records a continuum in the uplifting process and rate. It also negates the hypothesis suggested by Agustí et al. (2006) which contradicts the evidence indicated by pollen data. It seems that an important difference in altitude between the Cerdanya Basin and the surrounding massifs already occurred in the Late Miocene time and that the eastern Pyrenees structural block continued to uplift continuously since 10 Ma, its rate ranging from 0.06 to 0.12 mm/yr. These results contrast with the previous hypotheses of topography acquisition in the eastern Pyrenees (Quaternary activity of normal faults: Briais et al., 1990; Quaternary activity

of reverse faults: Philip et al., 1992; uplifted peneplain since the Late Miocene and subsequently eroded: Gunnell et al., 2009).

Concerning the palaeoaltitude estimation for the Canigou Mount, the method presented in this paper is based on the modern distribution of the *Abies–Picea* vegetation belt following the latitudinal and altitudinal thermal gradients. The distribution is somewhat crude since it depends on several parameters, such as exposure to sun, wind, soil, competition and, of course, of human activity. These trees may obviously develop at lower altitudes under favourable environmental conditions. However, the vegetation and the climate reconstructed for the eastern Pyrenees during the earliest Pliocene are very similar to those today in China at around 25°N latitude. Here, vegetation is organised into distinct vegetation belts (Fig. 7) and provides an idea of how the Pliocene vegetation in southern Europe could have been organised, according to altitude and latitude. In this modern southern Chinese vegetation organisation, *Abies* is found at high altitude, not below 1800 m (Wang, 1961; Zheng, 2000) (Fig. 7). Moreover, in the earliest Pliocene, the Roussillon shoreline occurred immediately at the foot of the mountains that significantly restricted the coastal plain width (Clauzon et al., 1990; Bache et al., 2011). Numerous low altitude taxa are recorded in the Le Boulou pollen assemblage. These taxa certainly colonised the slopes up to the mid-altitude, a situation that might have constrained *Abies* to very high altitude sites.

The presence of pollen grains of *Abies* in coastal marine sediments does not imply the presence of fir at low altitude. The present-day Grand Rhône prodeltaic sediments contain rare *Abies* pollen grains (<2%; Beaudouin et al., 2005), while the distance of the nearest populations exceeds 170 km (Fauquette et al., 1999). Modern pollen spectra from the eastern Pyrenees show the presence of pollen grains of *Abies* (*Picea* is not present today in the Pyrenean Mountains; Gaussen et al., 1972) in samples collected using the Cour's (1974) method (see above) from low- to mid- altitude sites at the foot of the Canigou Mount: (1) in the Mediterranean sclerophyllous vegetation (Ile sur Têt, 42°40'N–2°37'E, at 270 m a.s.l.; cf.: Supplementary data 1 and 2); (2) in the *Quercus pubescens* belt immediately beneath the lower limit of the beech series (Mosset, 42°41'N–2°19'E, at 900 m a.s.l.; cf.: Supplementary data 1 and 2). Thus, taking into account the pollen assemblages from Le Boulou, *Abies* should occur at high rather than at low- to mid- altitudes.

The method presented here does not aim to determine exact values for palaeoaltitudes because many uncertainties bias the results. The target is to try to give an idea of the existence or not of distinct relief and about its elevation at a given time. Comparison of reconstructed elevations at various times (including the present day) provides information concerning the tendency of evolution of the massifs (the continuing or relaxing uplift process, and the importance of erosion). Setting aside these uncertainties in relation to the MAT estimation, quantification of palaeoaltitude of uplifted sedimentary basins, such as the Cerdanya, provides relatively direct information although it is not possible to determine palaeoaltitude of the nearby summits. Palaeoaltitude of the latter can be approached through estimation of the palaeoaltitude of the base of the highest forest belt, the *Abies–Picea* belt in the case of this study. However, the approach presented here is highly indirect for determining palaeoaltitude of the massif concerned because: (1) it only indicates a minimum elevation of the relief, and (2) the difference from the actual palaeoaltitude cannot be evaluated. Indeed, if the forest culminated at the highest point reached by a massif, the difference could be relatively limited (some tens of metres) to moderate (up to 500 m, i.e. the width of the *Abies–Picea* belt; Fig. 9). Unfortunately, this matter cannot be resolved using pollen evidence. In addition, if an herbaceous belt covers the most elevated part of the massif, this difference is significantly increased because pollen analysis has yet to effectively detect such an alpine vegetation belt. Finally, this difference is further exacerbated where the summit was continuously covered by ice.

In this study the same lapse rate as today in Europe was used, i.e. 0.55 °C per 100 m in altitude. However, it should be noted that the terrestrial lapse rate may vary according to several factors such as atmospheric conditions, moisture, topography, season and continentality. In the example given here, continentality would not have modified the lapse rate since all the sites selected generally occurred in similar geographic conditions influenced by the nearby Mediterranean Sea. Topography may also be an important influence on the lapse rate. Since the palaeotopography of the region was not known *a priori*, it is impossible to determine its influence on the lapse rate, but the conclusion of an almost constant altitudinal shift between the localities studied and the surrounding massifs (Fig. 8) allowed such an effect to be set aside. Another factor leading to different lapse rates is the air moisture. A moist adiabatic lapse rate is close to 0.5 °C per 100 m, when the air is saturated, whereas the dry adiabatic lapse rate is 1 °C per 100 m if the air is unsaturated. During the Neogene periods studied, the climate was warm and humid. This indicated more or less saturated air conditions and thus a lapse rate of ca. 0.5 °C per 100 m. As a consequence, the average value established by Ozenda (1975, 1989) for Europe may be used in such studies with some caution.

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