

MESSINIAN AGE OF AN "OLIGOCENE" FOSSIL FLORA FROM ITALY

EDOARDO MARTINETTO^{1,*}, ANDREA IRACE², GIUSEPPE MARRAMÀ¹

¹ Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy;

e-mail: edoardo.martinetto@unito.it, giuseppe.marrama@unito.it.

² IGG-CNR Istituto di Geoscienze e Georisorse – Consiglio Nazionale delle Ricerche, Via Valperga Caluso 35, I-10125 Torino, Italy;

e-mail: andrea.irace@cnr.it.

*corresponding author

Martinetto, E., Irace, A., Marramà, G. (2024): Messinian age of an "Oligocene" fossil flora from Italy. – Fossil Imprint, 80(1): 161–180, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: An enigmatic deposit at Pavone d'Alessandria provided, at the end of the 19th century, about one hundred plant macrofossils, considered to be Oligocene in age. That material is no longer available, but a few animal (an insect and a fish) and plant remains have recently been recovered from this locality. A single remnant of *Aphanius crassicaudus* is considered relevant, in combination with a recent assessment of the geology in the studied area, to propose a Messinian age for the deposit. The taxonomic composition of the 19th century plant assemblage, only documented by sketchy drawings, is difficult to re-interpret, but its possible relationship with Messinian plant assemblages studied in the last 30 years is discussed in the light of recent observations. A few plant taxa that can be recognized on the basis of elementary morphological traits, e.g., *Fagus gussonii*, support a Messinian rather than Oligocene age.

Key words: Aphanius, fault, fossil leaves, geology, Neogene, Pavone d'Alessandria, Vena del Gesso

Received: May 16, 2024 | Accepted: July 20, 2024 | Issued: November 18, 2024

Introduction

In NW Italy, the Piemonte (Piedmont) region is rich in remains of Neogene flora (Bertini and Martinetto 2008, Martinetto et al. 2023), whereas Oligocene flora is exclusively documented at its southern border with the Liguria region (Peola 1900b, Charrier et al. 1964, Martinetto 2011). Therefore, the possibility to locate and study new Oligocene floras in more northern positions, e.g., in the Monferrato area (Text-fig. 1), could provide interesting information. A single Oligocene flora was reported by Peola (1900a) from eastern Monferrato. It has long been overlooked because of the very poor condition of the outcrop, with a consequent lack of geological and palaeontological information. Prof. Paolo Peola (1869–1947) lived, during the first part of his life, in Montecastello d'Alessandria (Peola 1899) and possibly paid much attention to the fossil plant remains reported around his home village. He occasionally found, and repeatedly sampled till exhaustion, a plant fossil assemblage from an ephemeral, very small outcrop in the bed of the Tanaro river at Pavone d'Alessandria (from here onwards, Pavone; Text-figs 1b, 2), in the neighbourhood of Montecastello d'Alessandria (Text-fig. 3). The same sedimentary body also yielded fish fossils that Peola (1900a: 58-59) sent to Prof F. Bassani, who interpreted them as "ciprindonti" [Cyprinodontidae?], related to the genus "Lebias CUVIER" (= Aphanius NARDO,

1827). Peola (1900a) wrote to keep the plant fossil material with him, and not in public collections, and presently it is unknown whether the collection still exists or not.

The first author of the present paper checked on the possibility of resampling the locality in the 1990s, but no outcrop was available at that time. In March 2022, an exceptionally long period of drought caused an extreme lowering of the Tanaro river water level, exposing sediments that are usually submerged. In the frame of a renewed interest in the cartographic representation of the area's geology (Pellegrino et al. 2020a, b, Irace et al. 2022), new field investigations along the left bank of the river showed some useful elements to better constrain the stratigraphic position of the fossil-bearing deposits described by Peola (1900a).

In summary, the aims of this work were to locate the historical plant-bearing deposit of Pavone, to obtain new samples, to revise the geological age of the deposit using new geological and palaeontological evidence and, finally, to attempt a taxonomical revision of the drawings by Peola (unpublished).

Geological setting

Pavone is situated in the eastern sector of the Piemonte region, in the eastern Monferrato reliefs (Text-fig. 1a, b),



Text-fig. 1. Location maps of the study area. a: Regional setting of Pavone di Alessandria site; trace of major buried thrust fronts of N Apennines also shown (modified after Frigerio et al. 2017). b: Geological sketch map of eastern Monferrato and adjoining Alessandria and Po alluvial plains (after Piana et al. 2017a). c: Simplified geological map of Pavone d'Alessandria site.

where the Cretaceous to Eocene External Ligurian Units are unconformably overlain by the Oligocene to Messinian sedimentary succession of the Tertiary Piemonte Basin (TPB), in turn unconformably followed by the Plio-Quaternary successions of the Alessandria and Padane Basins (Sacco 1890, Boni and Casnedi 1970, Dela Pierre et al. 2003a, b, Irace et al. 2010a, Piana et al. 2017a, b).

The Ligurian substratum is poorly exposed and crops out mainly within tectonic slices (Text-fig. 1b). The overlying TPB succession starts with unconformable fan-delta deposits (Cardona Formation, Rupelian) and prodelta slope sediments (Antognola Formation, Rupelian-Aquitanian). They are unconformably followed by carbonate ramp deposits (Pietra da Cantoni Formation, Burdigalian). Above another significant unconformity, inner shelf deposits (Tonengo sandstones, Langhian) mark the onset of a finingand deepening-upward trend (Casnedi 1975), evidenced by the overlying outer shelf (Mincengo Marls, Serravallian) to slope sediments (Sant'Agata Fossili Marls, Tortonian-Messinian), which record progressive restriction of the basin before the onset of the Messinian Salinity Crisis (hereafter, MSC). The Sant'Agata Fossili Marls consist of cyclically bedded hemipelagites (marls and silty clays) and are also characterised by diatomaceous deposits (Sturani and Sampò 1973, Pavia 1989, Gaudant et al. 2010, Pellegrino et al. 2020 a, b). New field investigations (see Frigerio et al. 2017), more recently related to the Geological Map of Italy at 1:50,000 scale (CARG Project, e.g., Irace et al. 2022), have highlighted the upward transition of the Sant'Agata Fossili Marls to a "euxinic" clayey succession consisting of thinly laminated shales and marls, and laterally discontinuous carbonate-rich layers. Subordinate primary gypsum laminae, some millimetres thick and made up of tiny acicular crystals, randomly oriented on the surface of the laminae, occasionally occur. Although the timing of these deposits is currently difficult to constrain, because of the lack of detailed bio-magnetostratigraphic investigations, their stratigraphic position and facies characters are very similar to those of the deeper water equivalents of the in-situ primary evaporites deposited during the first MSC phase (CIESM 2008, Dela Pierre et al. 2011, 2012). From a lithostratigraphic point of view, the clayey succession can be separated from the "normal" marine deposits of the Sant'Agata Fossili Marls and informally ascribed to the Nizza Monferrato Member of the Vena del Gesso Formation, previously recognized SW of the studied sector (Irace et al. 2010b, d'Atri et al. 2016). To the West, this syn-evaporitic succession is missing, as it is erosionally replaced by post-evaporitic chaotic gypsum deposits (Valle Versa chaotic Complex, sensu Dela Pierre et al. 2003a, b), of the second phase of the MSC (CIESM 2008). Conversely, in eastern Monferrato, it is unconformably topped by the post-evaporitic fan-delta to lacustrine deposits (Cassano-Spinola Conglomerates), recording the third MSC phase (CIESM 2008). The lower, erosional boundary of the Cassano-Spinola Conglomerates includes the tectonicenhanced intra-Messinian unconformity, encompassing the deposition of the chaotic deposits recorded in western Monferrato.

The Pliocene succession comprises outer shelf to slope deposits (Argille Azzurre, Zanclean) and peculiar shallow marine sediments, referred to as the Asti Sands. These were bio-chronologically constrained to the Zanclean-Piacenzian transition by Vannucci et al. (1994) through the integrated palaeontological study of some outcrops, located along the southwestern foothills of Monferrato, between Valle San Bartolomeo and Pavone (Text-fig. 1b). At the base of the Asti Sands, a definite intra-Zanclean erosional surface occurs, locally associated with an angular unconformity. The Pliocene succession is unconformably followed by Lower Pleistocene alluvial deposits which are, in turn, unconformably overlain by the Middle Pleistocene to Holocene terraced alluvial units.

The structural setting of the eastern Monferrato is mainly characterised by NE-verging thrust fronts, with an arcuate shape (Text-fig. 1a, b), and NW-SE trending, hm- to kmscale open to tight folds, affecting the whole Mesozoic-Pliocene succession (see Frigerio et al. 2017). Since the Early Miocene, the eastern Monferrato acted as a structural high between the Alessandria thrust-top Basin to the SW, and the Padane Basin to the NE. The evolution of this area was significantly controlled by the activity of the most external thrusts present in the Po Plain subsurface, as well as that of the internal ones, which are partly exposed in the present-day hills (Text-fig. 1b). During the Pliocene and Pleistocene, this tectonic activity induced the further uplift of the Monferrato Oligocene-Miocene successions and their NE-ward overthrusting onto the thicker Pliocene-Quaternary sedimentary pile of the Padane Basin.

Material and methods

Fieldwork, which included novel geological and palaeontological prospection and analysis, was carried out to reassess the poorly-known plant-bearing deposits sampled in the late 19th century by Peola. The left bank of the Tanaro river showed a large outcrop of strongly inclined Pliocene calcarenites (Text-figs 2a, 4a), followed eastwards by about 10 m without outcrops, but with sparse boulders of a fine sandstone, bearing a few leaf impressions (Text-fig. 5a). The next small outcrop showed rather chaotic, cemented, dominantly fine-grained sediments (Text-fig. 4b), bearing some animal and plant fossils. A few fossil specimens were recovered in the field and stored in the collections of the Museo di Geologia e Paleontologia at the Università degli Studi di Torino (MGPT).

For the few newly collected fossil remains, a Wild M3 dissecting microscope was used to observe finer details, and photos were taken using a Nikon Coolpix camera. The plant remains are fossilised as adpressions, with very scanty to null remains of organic matter, which do not seem to include cuticles when analysed under a stereomicroscope. Therefore, identification of leaves was based solely on macromorphological details. An arthropod remnant was compared to similar ones occurring in other Cenozoic sites of the Piemonte region, described by Cavallo and Galletti (1987). The traits of a fish remnant (Text-fig. 6) were interpreted using literature: Gaudant 1979, Parenti 1981, Carnevale et al. 2006, 2019, Caputo et al. 2009, Vasilyan et al. 2009, Bedosti et al. 2015, Carnevale and Schwarzhans 2022.

The most diverse fossil assemblage described from this site, consisting of plant fossils, is not available for revision



Text-fig. 2. a: Reconstructed field-line drawing showing intra-Zanclean angular unconformity between Oligocene-Miocene successions and Pliocene deposits, and NE-dipping backthrust (i.e., Pavone reverse fault (PF)) affecting entire succession (looking NW; see Text-fig. 1a for location). b: Line drawing of Google Earth aerial view showing Cardona Formation (Oligocene; CAD) tectonically juxtaposed to Nizza Monferrato Member (Messinian; VGS3), and Asti Sands (Pliocene; AST); asterisk indicates studied outcrop (see Text-fig. 1a for location).

(probably lost), but several sketchy drawings by Peola (unpublished) and his description of the site and its fossils (Peola 1900a) at the end of the 19th century have been considered useful materials that deserved to be re-analysed.



Text-fig. 3. Panoramic view of low hill of Pavone d'Alessandria with Tanaro river, from Montecastello d'Alessandria (NE to SW). Arrow indicates position of studied outcrop.

The reliability of the drawing by Peola has been checked for the first time against a few original fossil leaf specimens, not from Pavone, but from the Pliocene site of Bra (still very well preserved at the Craveri Museum of Bra; Text-fig. 7). Concerning the missing Pavone plant fossils, residual traits of leaf architecture visible in the drawings were checked against the macromorphological descriptions of Dilcher (1974) and Ellis et al. (2009). The outline and venation pattern of the leaf drawings have been analysed in an attempt to identify characteristic morphological traits that could throw some light on the taxonomic affinity of at least part of the plant remains. In any case, several leaves drawn by Peola were probably fragmented before sedimentation, so that the difficulties for their determination are increased by the original lack of information on the appearance of the whole leaf lamina.

Some tentative revised determinations (Tab. 1) could be proposed only by constraining the analysis to the types reported in the recent north Italian palaeobotanical literature on leaf assemblages from the Neogene (Bertini and Martinetto 2008, Brambilla and Gallo 2002, Denk 2004, Macaluso et al. 2018, Martinetto 2003, Martinetto et al. 2000, 2007, 2022, 2023, Teodoridis et al. 2015, 2017). Also relevant was a comparison to leaf morphotypes shown in a few other works from the Mediterranean area, dealing with almost contemporary leaf remains (Denk et al. 2017, Güner et al. 2017, Kvaček et al. 2002, Velitzelos 2002, Zidianakis et al. 2020). A few problematic specimens, which showed rather characteristic morphological traits in Peola's drawings, were compared to the type specimens of the taxa indicated by Peola (1900a), but also with other similar taxa of the European Cenozoic (Text-fig. 8). Finally, we indicated if Peola's determinations could be accepted or not (Tab. 1).

Results

Tectono-stratigraphic framework of the Pavone site

The Pavone di Alessandria area is characterised by a roughly SW-dipping Oligocene to Pliocene monocline (Text-fig. 1). Here the Asti Sands unconformably overlay the different terms of the monocline (from top to base: Argille Azzurre; Cassano-Spinola Formation; Nizza Monferrato Member of the Vena del Gesso Formation; Sant'Agata Fossili Marls; Cardona Formation). Two main fault systems (NW-SE and N-S to NNW-SSE directed) dissect the monocline (Text-fig. 1b). The former mainly corresponds to NE-vergent thrusts, which are parallel to the main thrust fronts, and here superpose the Cardona Formation onto the Sant'Agata Fossili Marls. The N- to NNW-striking system consists of high angle, transpressive to reverse faults, which probably worked as transfer fault.

The Pavone di Alessandria site (Text-fig. 1c) develops above one of the SW-ward verging backthrusts (i.e., a reverse fault with opposite vergence respect to the NEvergent main thrust surfaces). This structure, hereafter named the Pavone Fault (PF), juxtaposes the Oligocene succession to the Messinian euxinic deposits and Pliocene bioclastic sediments.

More in detail (Text-fig. 2), in the hanging wall of the PF, the lower Oligocene Cardona Formation strata are subhorizontal to gently (up to 20°) dipping toward SW. This

Table 1. List of fossil plant taxa cited by Peola (unpublished) for the Pavone d'Alessandria site and tentative taxonomic revision proposed here based on drawings of Text-figs 9–11.

Original determination and species number by Peola (1900a)	Revised determination	Peola (unpubl.), pl./fig.	This paper, Text-fig.
2. Taxites eumenidium A.MASSAL.	Coniferales indet.	4/6	Text-fig. 9q
3. Podocarpus oceanica Unger	cf. Pseudotsuga	4/8	Text-fig. 9f
4. Podocarpus gypsorum SAPORTA	Coniferales indet.	4/10	Text-fig. 9g
5. Podocarpus peyriacensis SAPORTA	Coniferales indet.	4/11	Text-fig. 91
6. Podocarpus taxiformis SAPORTA	Coniferales indet.	4/12	Text-fig. 9p
7. Sequoia couttsiae HEER	cf. Taiwania	5/1	Text-fig. 9c
7. Sequoia couttsiae HEER	cf. Cryptomeria vel Sequoia	5/1	Text-fig. 9d-e
8. <i>Sequoia langsdofii</i> (Brongn.) Heer	cf. Cryptomeria vel Sequoia	5/2	Text-fig. 9b
9. Sequoia sternbergii (Göpp.) HEER	cf. Cryptomeria vel Sequoia	5/5	Text-fig. 9a
10. <i>Sequoia tournalii</i> (Brongn.) Saporta.	cf. Taxodium dubium (Sternb.) A.BRAUN (less probable Sequoia)	5/9	Text-fig. 9i
11. Widdringtonia helvetica HEER	Most probably foliage of <i>Glyptostrobus europaeus</i> (BRONGN.) UNGER; the name <i>W. helvetica</i> HEER was introduced by Heer (1853) for a putative new species of conifer represented by a small shoot and a putative cone, later recognized respectively as a shoot of <i>Glyptostrobus</i> and as a fossil fruit of <i>Cercidiphyllum</i> (Jähnichen et al. 1980).	5/10	Text-fig. 9j
12. Libocedrus salicornioides (UNGER) HEER	indeterminable	5/13	Text-fig. 90
13. Chamaecyparites massiliensis (SAPORTA) SCHIMP.	cf. Glyptostrobus europaeus (BRONGN.) UNGER	5/16	Text-fig. 9k
14. Pinites cryptomeriodes A.MASSAL.	Coniferales indet.	5/17	Text-fig. 9n
15. – 21. <i>Pinus</i> spp.	<i>Pinus</i> spp. The fascicle with three needles and the fascicle with two long needles (Text-fig. 9u, w) can be assigned to <i>Pinus</i> cf. <i>rigios</i> (UNGER) ETTINGSH. (Text-fig. 9y), as discussed by Teodoridis et al. (2015). Other fascicles with two shorter or broken needles could belong to one or more separate species (e.g., <i>P. hepios</i> (UNGER) HEER).	6/1, 3, 4, 6, 9, 10; 7/6	Text-fig. 9r–y
22., 24. Pinus pseudotaeda SAPORTA and P. palaeostrobus (ETTINGSH.) HEER	<i>Pinus</i> cf. <i>palaeostrobus</i> (ETTINGSH.) HEER; fascicles of five thin needles (Text- fig. 9z, zb) suggest the occurrence of this species, as already discussed by Teodoridis et al. (2015).	8/5, 9	Text-fig. 9z, zb
23. Pinus quadrifoliata PEOLA	<i>Pinus</i> sp. The fascicle of four needles (Text-fig. 9za) can be interpreted either as an original morphology or as an incomplete five-needled fascicle that lost one needle. In the second case, regardless of the longer needles in comparison to the other two above-cited fascicles, it could be assigned to <i>P</i> . cf. <i>palaeostrobus</i> (ETTINGSH.) HEER. Although Peola (1900a) based a new species on this fossil, the description of the specimen (presently unavailable) does not seem to indicate morphological details that can justify the erection of a new taxon.	7/10	Text-fig. 9za
25. Abies piccottii Peola	Coniferales indet. (much unlikely to be <i>Abies</i> , due to the description of a very small petiole in Peola 1900a)	9/2	Text-fig. 9m
26. Abies? sp. ind.	Coniferales indet.	9/3	Text-fig. 9h
27. Panicum miocenicum Ettingsh.	Monocotyledones indet.	9/9	Text-fig. 11ze
28. Bambusa alexandrina PEOLA	<i>"Bambusa</i> " sp.; the leaf fragment corresponds morphologically to entire leaves assigned to <i>Bambusa</i> sp. by Teodoridis et al. (2015: pl. 4, figs 4, 5); the fragmentary specimen was inadequate to create a new species	10/7	Text-fig. 10a
29. Carpinus grandis Unger	<i>Carpinus</i> cf. <i>betulus</i> L.; the bract shows two lobes whose venation is characteristic for this living species, reported with several fossils at least since the Messinian (e.g., Bertini and Martinetto 2008, Martinetto 2015); <i>Carpinus grandis</i> UNGER is a name based on fossil leaves (fossil-species), which do not show relevant differences in comparison to those of the foregoing living species	13/4	Text-fig. 11f
29. Carpinus grandis Unger	cf. <i>Carpinus</i> ; the leaf fragment does not seem to show definite characters, apart the double serrulation, therefore the evidence is insufficient for sound assignment to the genus <i>Carpinus</i>	13/3	Text-fig. 11e
30. Fagus ambigua A.MASSAL.	Fagus gussonii A.MASSAL.	15/1	Text-fig. 10o
31. Fagus deucalionis UNGER	Fagus gussonii A.MASSAL.	16/2	Text-fig. 10g

Table 1. continued

Original determination and species number by Peola (1900a)	Revised determination	Peola (unpubl.), pl./fig.	This paper, Text-fig.
32. Quercus cornaliae A.MASSAL.	Quercus gr. pseudocastanea Göpp./Q. roburoides C.T.GAUDIN	20/6	Text-fig. 10n
33. Quercus scilliana C.T.GAUDIN	cf. Quercus pseudocastanea Göpp.	25/4	Text-fig. 11d
34. Myrica salicina UNGER	Indeterminable, but compatible with both Laurophyllum and Trigonobalanopsis.	30/6	Text-fig. 11c
35. Salix angusta A.BRAUN	cf. Salix	32/1	Text-fig. 11b
36. Salix media HEER	Salix sp. 1	32/8	Text-fig. 11m
37. Salix tenera A.BRAUN	indeterminable	32/12	Text-fig. 10d
38. Salix varians Göpp.	Salix sp. 2	32/14	Text-fig. 11p
39. Populus latior A.BRAUN	Populus latior A.BRAUN.	34/1	Text-fig. 10u
40. <i>Planera ungeri</i> Ettingsh.	cf. Zelkova zelkovifolia (UNGER) Bůžek et KOTL. (the name Planera ungeri is considered a synonym)	33/4	Text-fig. 11y
41. Ficus arcinervis HEER	cf. Leguminosae gen. et sp. indet. 1 of Teodoridis et al. (2015); this is the most probable identification, but it is also possible to indicate this morphotype as <i>"Ficus" arcinervis</i> (RossM.) HEER (because of the unknown taxonomic position, it is customary to assign <i>"Ficus"</i> as the genus). Less similar, for the arches of secondary veins closer to the margin, are Lauraceae and <i>Dicotylophyllum maii</i> BÚŻEK, HOLÝ et KVAČEK [never recorded in Italy]. Among extant plants, a strong resemblance to <i>Sabia</i> as for secondary venation can also be seen.	35/13	Text-fig. 10r
42. Ficus tiliaefolia HEER	cf. Fagus gussonii A.MASSAL.	37/2	Text-fig. 10p
43. Persea braunii HEER	cf. <i>Trigonobalanopsis rhamnoides</i> (ROSSM.) KVAČEK et H.WALTHER, a hypothesis supported by the analysis of the available Pliocene leaves from Bra (Martinetto et al. 2023); less probably <i>Laurophyllum</i> sp.	40/1	Text-fig. 10k
44. Persea speciosa HEER	cf. Trigonobalanopsis rhamnoides (Rossm.) KVAČEK et H.WALTHER, see above	40/4	Text-fig. 10j
44. Persea speciosa HEER	Indeterminable, remotely similar to <i>Laurophyllum</i> and <i>Magnolia</i> , too broad for <i>Trigonobalanopsis</i> .	40/3	Text-fig. 10b
45. Benzoin paucinerve HEER	Indeterminable, remotely similar to Laurophyllum sp. and Trigonobalanopsis.	41/6	Text-fig. 11v
46. Cinnamomum emarginatum SAPORTA	cf. Ocotea heeri (C.T.GAUDIN) W.R.MÜLL.	41/11	Text-fig. 11k
47. Cinnamomum lanceolatum SAPORTA	cf. Ocotea heeri (C.T.GAUDIN) W.R.MÜLL.	42/2	Text-fig. 10c
48. Cinnamomum polymorphum HEER	cf. Daphnogene polymorpha (A.BRAUN) ETTINGSH.	42/8	Text-fig. 11i
49. Cinnamomum rossmaessleri HEER	Daphnogene polymorpha (A.BRAUN) ETTINGSH.	42/14	Text-fig. 11h
50. Cinnamomum scheuczeri Heer	cf. <i>Ocotea heeri</i> (C.T.GAUDIN) W.R.MÜLL., alternatively <i>Laurophyllum pseudoprinceps</i> WEYL. et KILPPER, but not <i>Daphnogene polymorpha</i> (A.BRAUN) ETTINGSH.	42/16	Text-fig. 11j
51. Apeibopsis gaudinii HEER	cf. Carya fruit	45/7	Text-fig. 11q
52. Sterculia tenuinervis HEER	cf. <i>Acer integerrimum</i> VIV. in C.KEFERST.; the visible characters correspond to those of trilobate leaves assigned to the above-cited species, e.g., in Martinetto (2003: pl. 1 figs 11, 12) and Martinetto et al. (2023: fig. 18F); alternatively, it could be <i>Acer palaeosaccharinum</i> STUR or <i>Dombeyopsis lobata</i> UNGER, whereas <i>Sterculia</i> has not been confirmed by recent research in the Neogene of Piemonte.	46/2	Text-fig. 10t
53. Ptelea acuminata HEER	Indeterminable, but possibly similar to the leaf shown at Text-fig. 10h.	46/6	Text-fig. 101
54. Rhus pyrrhae Unger	Indeterminable, similar to <i>Rhus heufleuri</i> HEER, reported by Martinetto et al. (2000) for the Messinian of Alba, but in need of revision.	46/11	Text-fig. 11z
55. Acer primaevum Saporta	<i>Acer</i> sp.; many species represented by fruits are known from the Neogene of Europe, and specific research would be needed to assess the priority and validity of several names, e.g., <i>Acer primaevum</i> SAPORTA	47/6	Text-fig. 11r
56. Berchemia multinervis (A.BRAUN) HEER 57. Rhamnus rectinervis HEER	<i>"Juglans" acuminata</i> A.BRAUN eX UNGER – The narrow base and definite asymmetry are not typical characters for <i>Berchemia multinervis</i> (A.BRAUN) HEER, a species that occurs in Piemonte (Niccolini et al. 2022); in addition, Peola (1900a and unpubl.) never describes the typical tertiary venation. The lamina shape, dimensions and course of secondary veins agree much better with those of a lamina assigned to <i>Annona lortetii</i> SAPORTA by Brambilla and Gallo (2002); according to Denk (pers. comm.) this specimen from a neighbouring Messinian locality could be referred to <i>"Juglans" acuminata</i> A.BRAUN eX UNGER, a species indicated for the Messinian of northern Italy by Teodoridis et al. (2017). cf. <i>"Juglans" acuminata</i> A.BRAUN eX UNGER – see above	52/8	Text-fig. 10h Text-fig. 10i

Table 1. continued

Original determination and species number by Peola (1900a)	Revised determination	Peola (unpubl.), pl./fig.	This paper, Text-fig.
58. Weinmannia tetrasepala PEOLA	Indeterminable, it can be indicated as a specimen that was inadequate to create a new species.	54/6	Text-fig. 11za
59. Liquidambar europaea A.Braun	Liquidambar europaea A.BRAUN	54/7	Text-fig. 10m
60. Platanus depertita Sordelli.	<i>Platanus leucophylla</i> (UNGER) ERW.KNOBLOCH (the name <i>P. depertita</i> is considered as a synonym)	55/1	Text-fig. 10v
61. Terminalia elegans HEER	cf. Leguminosae gen. et sp. indet. 2 of Teodoridis et al. (2015); Peola (1900a) mentions poorly visible secondary veins, as is the case of the leaf shown by Teodoridis et al. (2015: pl. 5, fig. 9)	58/2	Text-fig. 10f
62. Terminalia radabojensis UNGER	cf. <i>Laurophyllum</i> ; the outline, dimension and course of secondary venation are identical to those of specimens of <i>Laurophyllum pseudoprinceps</i> WEYL. et KILPPER from Fossano (Macaluso et al. 2018); however, without any information about the cuticle, the similarity of the Pavone fossil to that fossil- species remains very speculative	59/1	Text-fig. 10s
63. Eucalyptus oceanica Unger	Indeterminable, but surely not <i>Eucalyptus</i> . Without secondary venation this narrow leaf is similar to several taxa, even if <i>Salix</i> could be the most parsimonious hypothesis.	59/5	Text-fig. 11a
64. Banksia laharpii HEER	cf. Rosaceae, e.g., <i>Rosa</i> (see Teodoridis et al. 2015: pl. 6, fig. 3) or <i>Sorbus</i> (see Kvaček et al. 2020)	54/18	Text-fig. 11t
65. Robinia regelii HEER	cf. Leguminosae	60/10	Text-fig. 11zc
66. Dalbergia cuneifolia HEER	Indeterminable, among several possibilities, the best match seems to be <i>Trigonobalanopsis rhamnoides</i> (ROSSM.) KVAČEK et H.WALTHER.	60/15	Text-fig. 11zg
67.Dalbergia jaccardii HEER	indeterminable	60/16	Text-fig. 11zf
68. Cassia berenices Unger	Indeterminable, among several possibilities it could be <i>Laurophyllum</i> , Leguminosae or <i>Trigonobalanopsis</i> .	61/10	Text-fig. 11zb
69. Cassia lignitum Unger	Indeterminable, among several possibilities, it could be <i>Laurophyllum</i> , Leguminosae or <i>Trigonobalanopsis</i> .	61/15	Text-fig. 11zd
70. Cassia zephyri Ettingsh.	Indeterminable, among several possibilities, it could be <i>Laurophyllum</i> , Leguminosae or <i>Trigonobalanopsis</i> .	61/22	Text-fig. 11n
71. Lucothoe protogaea Scн.	Indeterminable, among common Messinian taxa, it could be <i>Trigonobalanopsis, Laurophyllum</i> , Leguminosae or even <i>Salix</i> .	62/3	Text-fig. 11u
72. Lucothoe vacciniifolia UNGER	Indeterminable	62/7	Text-fig. 11g
73. Sapotacites eximius SAPORTA	cf. Leguminosae gen. et sp. indet. 2 of Teodoridis et al. (2015); the fine secondary and tertiary veins, only drawn at the bottom of the right side, agree with those of the leaf shown by Teodoridis et al. (2015: pl. 5, fig. 9); the acute versus rounded apex does not mean that this leaf must belong to a different species than the one of Text-fig. 10f	62/14	Text-fig. 10e
74. Diospyros varians SAPORTA	Indeterminable, among common Messinian taxa it could be, e.g., <i>Trigonobalanopsis rhamnoides</i> (Rossm.) Kvaček et H.Walther.	62/20	Text-fig. 11s
75. Styrax stylosus HEER	indeterminable	62/21	Text-fig. 11w
76. Olea proxima SAPORTA	indeterminable	63/7	Text-fig. 110
77. Fraxinus ulmifolia Saporta	cf. <i>Pterocarya paradisiaca</i> (UNGER) ILJINSK., whereas <i>Fraxinus</i> seems to be unlikely because of the densely packed, regular, small teeth; it is remotely similar to <i>Alnus gaudinii</i> (HEER) ERW.KNOBLOCH et KVAČEK as to leaf shape and secondary venation, but the teeth are too dense	63/8	Text-fig. 111
78. Apocinophyllum helveticum Heer	cf. Leguminosae gen. et sp. indet. 1 of Teodoridis et al. (2015). The identification is only tentative because the leaf was not described by Peola (1900a). The course of secondary veins as drawn by Peola (unpubl.) is not similar to that of the leaves of <i>Apocinophyllum helveticum</i> HEER. The discussion about specimen 35/13 can also be applied here, because the two leaves share the same basic traits.	64/1	Text-fig. 10q

unit consists of shallow marine coarse-grained sediments made up of conglomerates and partly burrowed yellowish to greenish sandstones in decimeter- to meter-thick beds. Clasts are mainly composed of ophiolitic bed-rocks and covers (serpentinites, gabbros, red-cherts, micritic limestones). During our field work we saw only bivalve fragments in sandy layers, poorly preserved. In the footwall of the PF, the Nizza Monferrato Member of the Vena del Gesso Formation is discontinuously exposed. Its bedding is mainly steeply inclined toward W and is sub-vertical close to the fault. This unit consists of a rhythmic alternation of thinly bedded and laminated dark grey-coloured shaley and fine sandy deposits, which here are intensively cemented. The most remarkable features of the



Text-fig. 4. Aspect of small outcrop of Pavone d'Alessandria on left bank of Tanaro river. a: Seen from bed of river (SW to NE); white arrow: Arenitic boulder with *Fagus* leaves (AST? Pliocene?); black arrow: Fossil-bearing outcrop of Messinian sediments (VGS3). b: Detail of stratified, fossil-bearing Messinian marls (VGS3). c: Seen from left bank of river (NE to SW) (see Text-fig. 2b for explanation).

succession are the well-developed thin stratification (beds are rarely thicker than 10 cm), the extremely thin lamination that mostly reflects changes in grain-size between laminae, and the complete absence of bioturbation. Some intervals of the laminated shales form strongly cemented dm-thick carbonate-rich layers, in which millimetre to centimetresized voids or calcite pseudomorphs after gypsum crystal are locally recognizable. Fossil content mainly consists of leaf adpressions. The original stratigraphic thickness of this unit cannot be estimated, because it is truncated by the tectonic boundary. The Nizza Monferrato Member is unconformably followed SW-ward (i.e., top of the section) by the Asti Sands, here comprising carbonate ramp biocalcirudites and biocalcarenites in dm- to cm-thick beds. The fossil content



Text-fig. 5. Fossils recently recovered from Pavone outcrop. a: *Fagus*, fragmentary leaf adpression on fine sandstone, retrieved from boulder in covered area, just below outcropping Pliocene succession, MGPT-PU141128. Occurrence of marine bivalves in these sediments suggests Pliocene succession origin (see Text-fig. 2a, AST?). b: Sediment sample from Messinian marls of Pavone outcrop (year 2022) with two badly preserved leaf adpressions, MGPT-PU141127; largest one likely *Quercus drymeja*, smaller one to right could be Leguminosae. c: Odonata, *Oryctodiplax*?; poorly preserved arthropod remnant (MGPT-PU141126) showing some similarities to pre-imaginal stages of fossil dragonfly *Oryctodiplax gypsorum* (Cavallo and Galletti 1987): Abdomen with 8 segments, two incomplete legs (arrow), last abdominal segment with anal appendages, and two darker spots in anterior part that could represent displaced eyes. d: Drawing of pre-imaginal fossil specimen of *Oryctodiplax gypsorum* from Cavallo and Galletti (1987), for comparison.

consists of calcareous red algae, bivalves, gastropods, brachiopods and foraminifera. The basal stratigraphic contact with the Vena del Gesso is associated with an about 40° inferred angular unconformity (Text-fig. 2a), which corresponds to an important hiatus encompassing the late Messinian and almost the whole Zanclean. Scattered boulders of arenites, not in place, containing *Fagus* leaves (Text-fig. 5a), were found near this unconformity at the river water level. The occurrence of marine bivalves in these sediments suggests an origin from the Pliocene succession.

Tentative taxonomic interpretation of Peola's plant drawings

In Peola (unpublished) we found 81 drawings of specimens originating from Pavone, mostly of leaves or leaf fragments, and only three carpological remains. The drawings provide at least one sketchy image of each of the 77 "species" of terrestrial plants (Tab. 1) listed in Peola's (1900a) monograph of the fossil flora of Pavone. Several of these names have been indicated, after Peola's paper (1900a), as synonyms of previous valid names (Tab. 1), e.g., in the case of *Widdringtonia helvetica* HEER, a name introduced by Heer (1853) for a small conifer shoot, later recognized as a shoot of *Glyptostrobus europaeus* (BRONGN.) UNGER (Jähnichen et al. 1980; actually, these authors considered

the name as valid for a co-occurring putative cone, revised as a fossil fruit of *Cercidiphyllum*, consequently named *C. helveticum* (HEER) JÄHNICHEN, MAI et H.WALTHER).

The reliability of the drawing by Peola has been checked, for the first time in this work, against a few original Pliocene leaf specimens still very well preserved at the Craveri Museum of Bra. The specimens appear as in a mirror (Textfig. 7), so that the drawings of Pavone's specimens were reflected horizontally in Text-figs. 9-11. The real leaf specimens from Bra show characters which were not reported in Peola's drawings (e.g., tertiary venation), and, generally, secondary venation and outline are reproduced with low precision. However, the secondary venation pattern, as drawn by Peola, is suitable to characterise the original one, as it is the outline. Teeth are reproduced in a very unreliable way in the leaf of Text-fig. 7a. Highly diagnostic characters were misinterpreted, such as the complete emarginate apex with attenuate midvein of the leaf, shown in Text-fig. 7d, drawn as a broken apex with an incomplete midvein. This analysis implies that only the dimensions, the secondary venation pattern and the outline could be used for a very tentative revised determination of Peola's Pavone drawings. Only a small proportion of the taxa reported in the Italian Neogene was suitable for an identification through these few characters.

Table 2. Revised determination of 52 specimens (missing material) drawn by Peola (unpublished) and shown in Text-figs 9–11, with reference to similar specimens illustrated in recent literature on Cenozoic leaf floras of Northern Italy.

This paper, Text-fig.	Revised determination	Peola's drawings (unpublished), original determination	Reference for comparison
Text-fig. 9a	cf. Cryptomeria vel Sequoia	Sequosia sternbergii	Teodoridis et al. 2015: pl. 1, fig. 7; Martinetto et al. 2022: pl. 1, fig. 3a
Text-fig. 9b	cf. Cryptomeria vel Sequoia	Sequoia langsdofii	Martinetto et al. 2022: pl. 1, fig. 5
Text-fig. 9c	cf. Taiwania	Sequoia couttsiae	Martinetto et al. 2022: pl. 1, fig. 1
Text-fig. 9d-e	cf. Cryptomeria vel Sequoia	Sequoia couttsiae	Martinetto et al. 2022: pl. 1, figs 2, 4, 5
Text-fig. 9f	cf. Pseudotsuga	Podocarpus oceanica	Martinetto et al. 2023: fig. 13A
Text-fig. 9i	cf. Taxodium dubium (less probable Sequoia)	Sequoia tournalii	Teodoridis et al. 2015: pl. 1, figs 9, 13
Text-fig. 9j	cf. Glyptostrobus europaeus	Widdringtonia helvetica	Teodoridis et al. 2015: pl. 1, fig. 11
Text-fig. 9k	cf. Glyptostrobus europaeus	Chamaecyparites massiliensis	Teodoridis et al. 2015: pl. 1, fig. 11
Text-fig. 9r-v, za	Pinus indet.	Pinus div. sp.	Teodoridis et al. 2017: figs 2/3–2/6
Text-fig. 9w, y	Pinus cf. rigios	Pinus div. sp.	Teodoridis et al. 2015: pl. 1, fig. 2
Text-fig. 9z, zb	Pinus cf. palaeostrobus	Pinus div. sp.	Teodoridis et al. 2015: pl. 1, fig. 4
Text-fig. 10a	"Bambusa" sp.	Bambusa alexandrina	Teodoridis et al. 2015: pl. 4, fig. 4
Text-fig. 10c	cf. Ocotea heeri	Cinnamomum lanceolatum	Teodoridis et al. 2015: pl. 2, fig. 9
Text-fig. 10e	cf. Leguminosae gen. et sp. indet.	Sapotacites eximius	Teodoridis et al. 2015: pl. 5, figs 6, 7
Text-fig. 10f	cf. Leguminosae gen. et sp. indet.	Terminalia elegans	Teodoridis et al. 2015: pl. 2, fig. 9
Text-fig. 10g	Fagus gussonii	Fagus deucalionis	Denk 2004: fig. 12K, M
Text-fig. 10h	"Juglans" acuminata	Berchemia multinervis	Teodoridis et al. 2017: fig. 9/4
Text-fig. 10i	cf. "Juglans" acuminata	Rhamnus rectinervis	Teodoridis et al. 2017: fig. 9/3
Text-fig. 10j	cf. Trigonobalanopsis rhamnoides	Persea speciosa	Teodoridis et al. 2015: pl. 2, fig. 4
Text-fig. 10k	cf. Trigonobalanopsis rhamnoides	Persea braunii	Martinetto et al. 2007: figs 4-37
Text-fig. 10m	Liquidambar europaea	Liquidambar europaea	Martinetto et al. 2007: figs 4-34
Text-fig. 10n	Quercus gr. pseudocastanea/roburoides	Quercus cornaliae	Teodoridis et al. 2015: pl. 7, fig. 12
Text-fig. 100	Fagus gussonii	Fagus ambigua	Teodoridis et al. 2015: pl. 2, fig. 10
Text-fig. 10p	Fagus gussonii	Ficus tiliaefolia	Teodoridis et al. 2015: pl. 8, fig. 11 (base of the leaf very similar)
Text-fig. 10q	cf. Leguminosae gen. et sp. indet.	Apocinophyllum helveticum	Teodoridis et al. 2015: pl. 5, fig. 12
Text-fig. 10r	cf. Leguminosae gen. et sp. indet.	Ficus arcinervis	Teodoridis et al. 2015: pl. 5, fig. 4
Text-fig. 10s	cf. Laurophyllum	Terminalia radabojensis	Martinetto 2003: pl. 5, fig. 6
Text-fig. 10t	cf. Acer integerrimum	Sterculia tenuinervis	Martinetto et al. 2023: fig. 18F
Text-fig. 10u	Populus latior	Populus latior	Martinetto 2003: pl. 7, fig. 5
Text-fig. 10v	Platanus leucophylla	Platanus depertita	Martinetto et al. 2007: figs 4-34
Text-fig. 11d	cf. Quercus pseudocastanea	Quercus scilliana	Martinetto 2003: pl. 4, fig. 7
Text-fig. 11e	cf. Carpinus	Carpinus grandis	Martinetto 2003: pl. 3, fig. 7
Text-fig. 11f	Carpinus cf. betulus	Carpinus grandis	Teodoridis et al. 2015: pl. 10, fig. 2
Text-fig. 11h	Daphnogene polymorpha	Cinnamomum rossmassleri	Martinetto et al. 2023: figs 11F, 16G
Text-fig. 11i	cf. Daphnogene polymorpha	Cinnamomum polymorphum	Teodoridis et al. 2015: pl. 3, fig. 2
Text-fig. 11j	cf. Ocotea heeri	Cinnamomum scheuczeri	Teodoridis et al. 2015: pl. 2, fig. 11
Text-fig. 11k	cf. Ocotea heeri	Cinnamomum emarginatum	Teodoridis et al. 2015: pl. 2, fig. 13
Text-fig. 111	cf. Pterocarya paradisiaca	Fraxinus ulmifolia	Teodoridis et al. 2015: pl. 9, fig. 7; Güner et al. 2017: pl. 7, fig. 4
Text-fig. 11m	Salix sp. 1	Salix media	Teodoridis et al. 2015: pl. 9, fig. 4
Text-fig. 11p	Salix sp. 2	Salix varians	Teodoridis et al. 2015: pl. 10, fig. 6
Text-fig. 11r	Acer sp.	Acer primaevum	Teodoridis et al. 2015: pl. 10, fig. 12
Text-fig. 11t	cf. Rosaceae	Banksia laharpii	Teodoridis et al. 2015: pl. 6, figs 4, 5
Text-fig. 11y	cf. Zelkova zelkovifolia	Planera ungeri	Teodoridis et al. 2015: pl. 7, fig. 1
Text-fig. 11zc	cf. Leguminosae	Robinia regelii	Teodoridis et al. 2015: pl. 5, figs 6, 7



Text-fig. 6. Fossil fish *Aphanius crassicaudus* AGASSIZ, 1848 recovered in Pavone outcrop, MGPT-PU 135802. a: Entire specimen. b: Close up of abdominal region showing tick epipleurals. c: Close up of caudal region. Scale bar 10 mm (a), 2 mm (b, c).

Comparison of Peola's Pavone drawings with Cenozoic fossil plant taxa described in north Italian literature (Bertini and Martinetto 2008, Bonci et al. 2011, Brambilla and Gallo 2002, Denk 2004, Hably 2010, Macaluso et al. 2018, Martinetto 2003, Martinetto et al. 2000, 2007, 2022, 2023, Teodoridis et al. 2015, 2017) led us to suggest the revised systematic placement of 52 specimens on the basis of definite morphological traits (Tab. 2). A few of them show traits that are useful for a less questionable determination, so that, in contrast with the 77 taxa identified by Peola (1900a), we confidently detected the occurrence of only 15 taxa (Tab. 1): Pinus cf. rigios (UNGER) ETTINGSH. (Text-fig. 9w, y), Pinus cf. palaeostrobus (ETTINGSH.) HEER (Text-fig. 9z, zb), Acer sp. (Text-fig. 11r, winged fruit), bambusoid grasses (Text-fig. 10a), Carpinus cf. betulus L. (Text-fig. 11f, fruit-bract), Daphnogene polymorpha (A.BRAUN) ETTINGSH. (Text-fig. 11h), Fagus gussonii A.MASSAL. (Text-fig. 10g, o), Liquidambar europaea A.BRAUN. (Text-fig. 10m), Ocotea cf. heeri (C.T.GAUDIN) W.R.Müll. (Text-fig. 10c), Populus latior A.BRAUN (Textfig. 10u), Platanus leucophylla (UNGER) ERW.KNOBLOCH, (Textfig. 10v), Quercus gr. pseudocastanea Göpp./Q. roburoides C.T.GAUDIN (Text-fig. 10n) and Salix (Text-fig. 11p).

The last confidently identified taxon is represented by a 7 cm long lamina (Text-fig. 8a) with characteristic secondary venation, which was subjected to particularly detailed comparisons. It was assigned by Peola (1900a) to Berchemia multinervis (A.BRAUN) HEER, but the leaves of such species are generally shorter than 5 cm, with less arched secondary veins, not running along the margin towards the leaf tip (Text-fig. 8b). The Pavone specimen shows more analogies with a fossil leaf from the Pliocene of Lombardy (Text-fig. 8c - 10 cm long without petiole), assigned by Sordelli (1896) to Annona lortetii SAPORTA, and another from the Messinian of Nizza Monferrato (Textfig. 8g), also assigned to Annona lortetii by Brambilla and Gallo (2002). However, the observation of both the detailed drawing by Saporta et al. (1872: 272, pl. 32, fig. 5) and the original specimen of Annona lortetii at the MNHN of Paris evidenced a quite different pattern of tertiary veins (Textfig. 8d, e). The three Italian fossil leaves (Text-fig. 8a, c, g) may well belong to a single taxon, but it is not Annona lortetii. A major similarity in overall leaf characters, and tertiary venation pattern in particular, was detected with specimens (Text-fig. 8h) assigned to "Juglans" acuminata



Text-fig. 7. Comparison of two drawings of Peola (unpubl.) with real fossil specimens from Pliocene site of Bra (Martinetto et al. 2023). a: Drawing of basal part of leaf fragment assigned by Peola (1896) to "*Castanea tornabenii* A.MASSAL.". b: Fossil specimen corresponding to drawing in (a), assigned to *Quercus gigas* Göpp. by Martinetto et al. (2023). c: Drawing of fossil leaf assigned by Peola (1896) to *Quercus cyclophylla* UNGER. d: Fossil specimen corresponding to drawing in (c), assigned to *Alnus ducalis* (C.T.GAUDIN) ERW.KNOBL. by Martinetto et al. (2023). Scale bar 1 cm.

A.BRAUN ex UNGER (Heer 1859: pls. 128, 129, Ludwig 1860: pl. 56, figs 2, 4, 6, pl. 57, fig. 6 [as "Juglans costata C.PRESL ex UNGER"], Teodoridis et al. 2017: fig. 9/4). This name is associated with a very variable type of leaflets of problematic systematic placement (Kvaček and Hurník 2000, Kvaček et al. 2011). In recent works, it has been considered as non-related to the Juglandaceae, and Kvaček et al. (2020) indicated an assignment to Meliaceae (e.g., Cedrela: Text-fig. 8f). Although the leaflets of "Juglans" acuminata are generally narrower and have an acuminate tip, the known range of variability (Heer 1859: pls 128, 129) also includes larger leaflets with a more obtuse tip, as in Sordelli's specimen (Text-fig. 8c). Therefore, we concluded that the most consistent assignment of the Pavone specimen (Text-fig. 8a) and the two similar ones (Text-fig. 8c, g) is to "Juglans" acuminata (Meliaceae).

Concerning the 13 other Pavone specimens, we just mention a possible similarity with genera or fossil-species reported in the Neogene of northern Italy (names preceded by "cf."), most of whose diagnostic traits cannot be detected fig. 11q - possible endocarp), cf. Cryptomeria vel Sequoia (Text-fig. 9a, b, d, e), cf. *Glyptostrobus europaeus* (BRONGN.) UNGER (Text-fig. 9j, k), cf. Taiwania (Text-fig. 9c), cf. Taxodium dubium (STERNB.) A.BRAUN (Text-fig. 9i), cf. Acer integerrimum VIV. (Text-fig. 10t), cf. Carpinus (Textfig. 11e), cf. Laurophyllum (Text-fig. 11s), cf. Leguminosae (Text-figs 10q, 11zc), cf. "Juglans" acuminata (Textfig. 10i), cf. Pterocarya paradisiaca (UNGER) ILJINSK. (Textfig. 11m), cf. Rosaceae (Text-fig. 11t), cf. Trigonobalanopsis rhamnoides (Rossm.) Kvaček et H. Walther (Text-fig. 10j, k) and cf. Zelkova zelkovifolia (UNGER) Bůžek et KOTL. (Textfig. 11y). Systematic interpretation of the smaller leaves is mostly impossible (Text-fig. 11), because their drawings do not show diagnostic characters: We can single out (Tab. 1) only individual specimens of cf. Daphnogene polymorpha, cf. Ocotea heeri (C.T.GAUDIN) W.R.MÜLL. and cf. Salix (taxa already reported above).

with certainty in Peola's drawings: cf. Carya (Text-

Newly recovered fossils

At the Pavone outcrop (Text-fig. 2), leaf-bearing sediments have been detected in thinly, flat-layered pelites, dipping at steep angles (Nizza Monferrato Member, VGS3 in Text-figs 2, 4). A portion of these sediments yielded adpressions of a few conifer and dicotyledonous-type leaves (Text-fig. 5b), an arthropod remnant (Text-fig. 5c) and a small portion of a fish tail. 2 m northwards, an almost complete external cast of a fish body was recovered (Textfig. 6) from a stratigraphic position roughly corresponding to that of the plant- and arthropod-bearing layer.

Plant fossils

The best-preserved plant remains retrieved from the Nizza Monferrato Member of the Pavone outcrop (Text-fig. 2) were two laminae (Text-fig. 5b) on a single sediment sample (MGPT-PU141127). The largest leaf has a characteristic outline, secondary venation and teeth type, which suggest Quercus drymeja UNGER (see Denk et al. 2017: pl. 4, fig. 1), a fossil-species which occurs in the Neogene of northern Italy, where only a few specimens have been found. Its rarity supports a random occurrence, and may explain why it is not present in Peola's drawings (1900a). The second, smaller lamina does not correspond to any of Peola's drawings (1900a), but its sub-rounded shape and fine secondary venation suggest that it could be a leaflet from a member of Leguminosae (Denk et al. 2017: pl. 3, fig. 9), not particularly similar to the types recognized on the basis of drawings (Text-figs 10e, f, g, r, 11za). An admissible alternative would be a small, entire margined leaf of Quercus mediterranea UNGER (see Velitzelos 2002: pl. 16, fig. 9).

Arthropod fossil

The arthropod remnant (MGPT-PU141126) is poorly visible on the sedimentary matrix because a minor portion of the exoskeleton was preserved (Text-fig. 5c), but the detectable morphology shares significant characters with the pre-imaginal stages of *Oryctodiplax gypsorum* CAVALLO et GALLETTI (Text-fig. 5d), as described by Cavallo and Galletti (1987): dimension, breadth and oval outline of the



Text-fig. 8. Comparison of drawing of fossil leaf from Pavone (a), assigned by Peola (1900a) to *Berchemia multinervis* (A.BRAUN) HEER, with other fossil and extant specimens. b: *Berchemia multinervis* (A.BRAUN) HEER (Heer 1859: pl. 123, fig. 14). c: specimen from Pliocene of Lombardy assigned to *Annona lortetii* SAPORTA by Sordelli (1896). d: original specimen of *Annona lortetii*, courtesy of MNHN of Paris (Saporta et al. 1872). e: drawing based on foregoing specimen in Saporta et al. (1872: 272, pl. 32, fig. 5). f: leaflet of extant *Cedrela montana* J.MORITZ ex TURCZ. (from Peru), courtesy of Missouri Botanical Garden Herbarium. g: specimen from Messinian of Nizza Monferrato assigned to *Annona lortetii* SAPORTA by Brambilla and Gallo (2002). h: specimen from Miocene of Germany, treated as "*Juglans costata* C.PRESL ex UNGER" by Ludwig (1860).

abdomen with 8 segments, length and thickness of the legs, length of last abdominal segment and dimensions of the anal appendages. The head is not visible, but two darker spots could represent the displaced eyes, which would agree with those of Cavallo and Galletti's (1987) fossils in dimension and distance among them. This arthropod remnant can be assigned to the order Odonata and possibly to the genus *Oryctodiplax*.

Fish fossil

Subdivision Teleostei Müller 1845 sensu Patterson and Rosen (1977)

Order Cyprinodontiformes BERG, 1940 sensu Parenti (1981) Family Cyprinodontidae Agassiz, 1834

Genus Aphanius Nardo, 1827

Aphanius crassicaudus Agassiz, 1839 Text-fig. 6

M at er i a l. Specimen (MGPT-PU135802) is a small, articulated and partially incomplete skeleton, lacking the head and the distalmost margin of the caudal fin (Text-fig. 6). The preserved skeleton is 39.8 mm in length, with a maximum body depth at dorsal-fin origin of 10.3 mm.



Text-fig. 9. Drawings of Messinian plant fossils from Pavone (Peola unpublished). a: cf. *Cryptomeria* vel *Sequoia*, as *Sequoia* sternbergii in Peola (unpubl.). b: cf. *Cryptomeria* vel *Sequoia*, as *Sequoia langsdofii* in Peola (unpubl.). c: cf. *Taiwania*, as *Sequoia couttsiae* in Peola (unpubl.). d, e: cf. *Cryptomeria* vel *Sequoia*, as *Sequoia couttsiae* in Peola (unpubl.). f: cf. *Pseudotsuga*, as *Podocarpus oceanica* in Peola (unpubl.). g: Coniferales indet., as *Podocarpus gypsorum* in Peola (unpubl.). h: Coniferales indet., as *Abies*? sp. ind. in Peola (unpubl.). i: cf. *Taxodium dubium* (less probable *Sequoia*), as *Sequoia tournalii* in Peola (unpubl.). j: cf. *Glyptostrobus europaeus*, as *Widdringtonia helvetica* in Peola (unpubl.). k: cf. *Glyptostrobus europaeus*, as *Chamaecyparites massiliensis* in Peola (unpubl.). l: Coniferales indet., as *Podocarpus peyriacensis* in Peola (unpubl.). m: Coniferales indet., as *Abies piccottii* in Peola (unpubl.). l: Coniferales indet., as *Podocarpus peyriacensis* in Peola (unpubl.). m: Coniferales indet., as *Abies piccottii* in Peola (unpubl.). l: Coniferales indet., as *Podocarpus peyriacensis* in Peola (unpubl.). m: Coniferales indet., as *Podocarpus peyriacensis* in Peola (unpubl.). m: Coniferales indet., as *Abies piccottii* in Peola (unpubl.). p: Coniferales indet., as *Podocarpus taxiformis* in Peola (unpubl.). q: Coniferales indet., as *Podocarpus taxiformis* in Peola (unpubl.). q: Coniferales indet., as *Taxites eumenidium* in Peola (unpubl.). p: *Pinus* indet., as *Pinus* div. sp. in Peola (unpubl.). w–y: *Pinus* cf. *rigios*, as *Pinus* div. sp. in Peola (unpubl.). w–y: *Pinus* cf. *rigios*, as *Pinus* div. sp. in Peola (unpubl.). z–zb: *Pinus* cf. *palaeostrobus*, as *Pinus* div. sp. in Peola (unpubl.). Scale bar 1 cm.

Description. The body of the fossil specimen is laterally compressed, moderately elongate and shallow, with nearly straight dorsal and abdominal profiles (Text-fig. 6a). The caudal peduncle is short and stocky, with its height about two-thirds of its length. There are 24 vertebrae preserved, but it is likely that their original number was higher, being the anteriormost portion of the vertebral column not preserved. Of these, 16 vertebrae are caudal. The centra are subrectangular, longer than high and characterised by a high degree of hyperostosis of their neural and haemal arches and spines, these latter being posteriorly oriented with an angle measuring about 45°. At least seven epipleurals can be recognized on the posteriormost abdominal vertebrae (Text-fig. 6b): they are short, remarkably thick, nearly fusiform and not bifid, with their distal margin posterodorsally directed. Dorsal and anal fins are short based. The dorsal fin is located at about mid-length, with its origin being clearly anterior to the anal fin, this latter originating below the perpendicular to posterior end of the dorsal fin. There are 10 or 11 dorsal-fin rays and 9 or 10 anal-fin rays, both supported by an equal number of pterygiophores. The pelvic fins are small and placed anteriorly to the dorsal-fin origin, with about six rays. The caudal-fin skeleton has all hypural plates fused into a single hypural fan (Text-fig. 6c). The caudal fin is incomplete in its distalmost margin, but at least 28 caudal-fin rays (15 principals + 13 procurrent) can be counted in its proximal part. Body scales are mostly not preserved, but large and thick scattered cycloid scales cover part of the dorsal and ventral margins of the body.

Despite its incompleteness, the fossil preserves many features that support its inclusion in the cyprinodontid genus Aphanius, including the general body physiognomy and its small size, hypural plates fused into a hypural fan, presence of an undivided dorsal fin positioned slightly in front of the anal fin, epipleurals not bifid, and meristic count ranges consistent with that of the genus (Parenti 1981, Vasilyan et al. 2009). Moreover, the specimen exhibits a combination of features that support its alignment with the species A. crassicaudus AGASSIZ, 1848, an euryhaline estuarine species widespread in the Mediterranean basin throughout the Messinian (e.g., Carnevale et al. 2006, 2019, Caputo et al. 2009, Reichenbacher and Kowalke 2009, Carnevale and Schwarzhans 2022). These traits include the number of caudal vertebrae (16), dorsal- and anal-fin rays (10-11 and 9-10, respectively), caudal-fin rays (28+), and hyperostosis that often characterises the bones A. crassicaudus as evident enlargement of the bone structures (Gaudant 1979, Parenti 1981, Vasilyan et al. 2009, Bedosti et al. 2015).

Discussion and conclusions

Even if there is not a single specimen of Peola's plant fossils from Pavone which is still available, we argue, on the basis of the occurrence of fish fossils related to *Aphanius*



Text-fig. 10. Drawings of Messinian plant fossils from Pavone (Peola unpublished). a: "Bambusa" sp., as Bambusa alexandrina in Peola (unpubl.). b: Indeterminable, as Persea speciosa in Peola (unpubl.). c: cf. Ocotea heeri, as Cinnamomum lanceolatum in Peola (unpubl.). d: Indeterminable, as Salix tenera in Peola (unpubl.). e: cf. Leguminosae gen. et sp. indet., as Sapotacites eximius in Peola (unpubl.). f: cf. Leguminosae gen. et sp. indet., as Terminalia elegans in Peola (unpubl.). g: Fagus gussonii, as Fagus deucalionis in Peola (unpubl.). h: "Juglans" acuminata, as Berchemia multinervis in Peola (unpubl.). i: cf. "Juglans" acuminata, as Rhamnus rectinervis in Peola (unpubl.). j: cf. Trigonobalanopsis rhamnoides, as Persea speciosa in Peola (unpubl.). k: cf. Trigonobalanopsis rhamnoides, as Persea braunii in Peola (unpubl.). l: Indeterminable, as Ptelea acuminata in Peola (unpubl.). m: Liquidambar europaea, as Liquidambar europaea in Peola (unpubl.). n: Quercus gr. pseudocastanea / Q. roburoides, as Quercus cornaliae in Peola (unpubl.). o: Fagus gussonii, as Fagus ambigua in Peola (unpubl.). p: cf. Fagus gussonii, as Ficus tiliaefolia in Peola (unpubl.). q: cf. Leguminosae gen. et sp. indet., as Apocinophyllum helveticum in Peola (unpubl.). r: cf. Leguminosae gen. et sp. indet., as Ficus arcinervis in Peola (unpubl.). s: cf. Laurophyllum, as Terminalia radabojensis in Peola (unpubl.). t: cf. Acer integerrimum, as Sterculia tenuinervis in Peola (unpubl.). u: Populus latior, as Populus latior in Peola (unpubl.). v: Platanus leucophylla, as Platanus depertita in Peola (unpubl.). Scale bar 1 cm.

and of the descriptions of plant fossils he published (Peola 1900a), that his material could have come from sediments similar to the leaf-bearing ones we observed in the field during the year 2022 (Nizza Monferrato Member). Considering the local lithostratigraphy and palaeontological assemblages, the occurrence of a dragonfly larva and a cast of *Aphanius crassicaudus* suggests that these sediments could belong to the first MSC phase (Dela Pierre et al. 2016). At least one plant fossil-species, recognized on the basis of Peola's (1900a) drawings, supports a Messinian rather than Oligocene age: *Fagus gussonii* A.MASSAL. has

never been reported from the Oligocene anywhere in the entire Mediterranean area (Denk 2004). The plant-bearing sediment of Pavone is more likely Messinian rather than "Tongrian" (i.e., Oligocene), as was suggested by Peola (1900a). A Messinian locality with similar lithologies and fossils is known only 16 km to the SE in the bed of the Scrivia river (Brambilla et al. 1982).

Even if the occurrence of fossil leaves originating from Pliocene sediments was observed by us in the Pavone outcrop (Text-fig. 5a), Peola (1900a: 37) firmly stated that the plant fossils described by him were collected from a single



Text-fig. 11. Drawings of Messinian plant fossils from Pavone (Peola unpublished). a: Indeterminable, as Eucalyptus oceanica in Peola (unpubl.). b: cf. Salix, as Salix angusta in Peola (unpubl.). c: Indeterminable, as Myrica salicina in Peola (unpubl.). d: cf. Quercus pseudocastanea, as Quercus scilliana in Peola (unpubl.). e: cf. Carpinus, as Carpinus grandis in Peola (unpubl.). f: Carpinus cf. betulus, as Carpinus grandis in Peola (unpubl.). g: Indeterminable, as Lucothoe vacciniifolia in Peola (unpubl.). h: Daphnogene polymorpha, as Cinnamomum rossmaessleri in Peola (unpubl.). i: cf. Daphnogene polymorpha, as Cinnamomum polymorphum in Peola (unpubl.). j: cf. Ocotea heeri, as Cinnamomum scheuczeri in Peola (unpubl.). k: cf. Ocotea heeri, as Cinnamomum emarginatum in Peola (unpubl.). I: cf. Pterocarya paradisiaca, as Fraxinus ulmifolia in Peola (unpubl.). m: Salix sp. 1, as Salix media in Peola (unpubl.). n: Indeterminable, as Cassia zephyri in Peola (unpubl.). o: Indeterminable, as Olea proxima in Peola (unpubl.). p: Salix sp. 2, as Salix varians in Peola (unpubl.). q: cf. Carya fruit, as Apeibopsis gaudinii in Peola (unpubl.). r: Acer sp., as Acer primaevum in Peola (unpubl.). u: Indeterminable, as Lucothoe protogaea in Peola (unpubl.). v: Indeterminable, as Benzoin paucinerve in Peola (unpubl.). w: Indeterminable, as Styrax stylosus in Peola (unpubl.). y: cf. Zelkova zelkovifolia, as Planera ungeri in Peola (unpubl.). z: Indeterminable, as Rhus pyrrhae in Peola (unpubl.). za: Indeterminable, as Weinmannia tetrasepala in Peola (unpubl.). zb: Indeterminable, as Cassia berenices in Peola (unpubl.). zc: cf. Leguminosae, as Robinia regelii in Peola (unpubl.). zd: Indeterminable, as Cassia lignitum in Peola (unpubl.). ze: Monocotyledones indet., as Panicum miocenicum in Peola (unpubl.). zf: Indeterminable, as Dalbergia jaccardii in Peola (unpubl.). zg: Indeterminable, as Dalbergia cuneifolia in Peola (unpubl.). Scale bar 1 cm.

marly-arenaceous body ("in uno di questi banchi marnosoarenacei"), which also yielded some fish (*Aphanius*?). Both the lithology and the occurrence of *Aphanius*? indicate that the sedimentary body he sampled was most likely part of the Nizza Monferrato Member.

Therefore, Peola's descriptions (1900a) and drawings (unpublished) can be referred to a Messinian plant assemblage that showed a considerable diversity of conifers (Text-fig. 9), among which are at least two types of *Pinus* foliage and some cupressoid, cryptomerioid and taxodioid shoots. The drawn Angiosperm leaves are mostly fragmentary. A smaller part shows almost complete laminae, even of large leaves (Text-fig. 10). Despite the uncertain systematic placement, they clearly show a diversity of morphotypes, suggesting that each plant taxon of the source vegetation produced one or a few specimens, buried together after considerable transport. Remarkably, one of the two recently recovered leaves is from a previously unrecorded taxon (*Quercus drymeja*). This kind of assemblage containing *Daphnogene polymorpha, Fagus gussonii, Liquidambar europaea, Ocotea heeri, Platanus*

leucophylla, Populus latior, etc., is similar from both the taphonomic and taxonomic point of view to most of the assemblages referred to the first MSC phase in northern Italy (Bertini and Martinetto 2008, Brambilla and Gallo 2002, Martinetto et al. 2000, 2007, 2023, Teodoridis et al. 2015, 2017).

Peola's (1900a) Pavone work has just been cited in a few non-Italian palaeobotanical papers (Worobiec and Worobiec 2005, Wang et al. 2013, 2014, Srivastava et al. 2019). However, we deem it useful to underline the wrongly suggested age of the palaeoflora of Pavone in order to prevent a misuse of these published records. Actually, this already happened for the oldest record of bamboos in Europe, indicated by Srivastava et al. (2019) as being "from the Oligocene of Italy", with special reference to Peola (1900a) and therefore to fossils from Pavone.

In reading Peola's (1900a) conclusions, it would appear that the fossil flora of Pavone may have considerable significance, due to its purported diversity (77 species; Tab. 1). However, we see this author as having a tendency to separate different species on the basis of minor differences that are actually merely variations within a species (see Martinetto et al. 2023, for the Pliocene flora of Bra), and we presume that, even if the Pavone plant remains had been better preserved and still available, they would still not sum up to more than a few tens of species. Furthermore, from Peola's descriptions (no photos, only drawings), it would seem that the state of preservation of his specimens was not good. This same poor preservation is also observed in the newly collected samples (Text-fig. 5c). Therefore, considering the richness of the Messinian floras in the Piemonte region (Martinetto et al. 2007, 2022, 2023) and the poor quality of preservation of the Pavone specimens, further recovery of fossils from this outcrop should not be considered a priority.

Finally, this study is a representative example of how detailed field mapping studies can produce tectonostratigraphic reconstructions that can be helpful for the chronostratigraphic framing of palaeofloras, above all in those areas with poor rock exposures.

Acknowledgements

We thank Giorgio Carnevale for his constructive advice on fish description, Emilia Cianci for bibliographic assistance in the Malaroda Library of the Università degli Studi di Torino, Luca Pellegrino for useful information and help in recovering the studied fossil fish; Thomas Denk for discussions about the systematic interpretation of Peola's drawings and for the suggestions about "Juglans" acuminata; Cédric Del Rio for the study of specimens at the MNHN of Paris, for sending useful images and for revision of the manuscript; Carlos A. Góis-Marques for his comments and suggestions, which allowed us to substantially improve the manuscript. We are grateful to Marco Pavia, keeper of the Museo di Geologia e Paleontologia collections at the Università degli Studi di Torino, for informing us that this is publication number 371 dealing with specimens of that collection. The research was supported by grants (ex-60 % 2021 and 2022) from the Università degli Studi di Torino and by the CNR-Istituto di Geoscienze e Georisorse, Sede Secondaria di Torino (IGG-TO), in the framework of the sheet 177 Tortona of the Geological Map of Italy at 1:50,000 scale (CARG Project).

References

- Bedosti, N., Landini, L., D'Anastasio, R. (2015): The increase of bony mass in a small Cyprinodontidae from the Messinian deposit of Monte Tondo (Ravenna, Italy); paleoecological implications. – Atti Società Toscana Scienze Naturali, Memorie, Serie A, 122: 5–17.
- Bertini, A., Martinetto, E. (2008): Messinian to Zanclean vegetation and climate of Northern and Central Italy. Bollettino della Società Paleontologica Italiana, 47(2): 105–121.
- Bonci, M. C., Vannucci, G., Tacchino, S., Piazza, M. (2011): Oligocene fossil leaves of the Perrando Collection: History, preservation, and paleoclimatic meaning. – Bollettino della Società Paleontologica Italiana, 50(3): 145–164.

- Boni, A., Casnedi, R. (1970): Note Illustrative della Carta Geologica d'Italia, alla scala 1:100.000. Fogli 69 e 70, Asti-Alessandria [Explantory Notes of the Geological Map of Italy, scale 1:100,000. Sheets 69 and 70, Asti-Alessandria]. – Ed. Poligrafica e Cartevalori, Ercolano, 64 pp. (in Italian)
- Brambilla, G., Gallo, M. (2002): Analisi stratigrafica e paleobotanica della successione messiniana di Bric Santa Margherita (Nizza Monferrato, Asti, Italia NW) [Stratigraphic and palaeobotanical analysis of the Messinian succession of Bric Santa Margherita (Nizza Monferrato, Asti, NW Italy)]. Bollettino del Museo Regionale di Scienze Naturali di Torino, 19(1): 191–283. (in Italian)
- Brambilla, G., Ronchetti, G., Vittadini Zorzoli, M. (1982): Semi e filliti delle argille messiniane (Miocene superiore) di Carbonara Scrivia (Alessandria) [Seeds and fossil leaves from the Messinian clays (Upper Miocene) of Carbonara Scrivia (Alessandria)]. – Atti dell'Istituto Botanico e Laboratorio Crittogamico di Pavia, 1: 31–40. (in Italian)
- Caputo, D., Carnevale, G., Landini, W. (2009): Fish otoliths from the Messinian of Strada degli Archi (Tuscany, Italy) – Taxonomy and paleoecology. – Annalen des Naturhistorischen Museums, Wien, A, 111: 257–280.
- Carnevale, G., Gennari, R., Lozar, F. Natalicchio, M., Pellegrino, L., Dela Pierre, F. (2019): Living in a deep desiccated Mediterranean Sea: An overview of the Italian fossil record of the Messinian salinity crisis. – Bollettino della Società Paleontologica Italiana, 58: 109–140.
- Carnevale, G., Landini W., Sarti, G. (2006): Mare versus Lago-mare: Marine fishes and the Mediterranean environment at the end of the Messinian Salinity Crisis. – Journal of the Geological Society, London, 163: 75–80. https://doi.org/10.1144/0016-764904-158
- Carnevale, G., Schwarzhans, W. (2022): Marine life in the Mediterranean during the Messinian salinity crisis: a paleoichthyological perspective. – Rivista Italiana di Paleontologia e Stratigrafia, 128(2): 283–324. https://doi.org/10.54103/2039-4942/15964
- Casnedi, R. (1975): Segnalazione di una successione stratigrafica compresa fra il Langhiano e il Pliocene inferiore a NW di Valenza (Monferrato orientale) [Report of a stratigraphic succession straddling the Langhian and the Lower Pliocene to the NW of Valenza (eastern Monferrato)]. – Rendiconti, Classe di scienze, Istituto lombardo, Accademia di scienze e lettere, 109: 178–184. (in Italian)
- Cavallo, O., Galletti, P. A. (1987): Studi di Carlo Sturani su Odonati e altri insetti fossili del Messiniano albese (Piemonte) con descrizione di *Oryctodiplax gypsorum* n. gen. n. sp. (Odonata, Libellulidae) [Studies by Carlo Sturani on Odonates and other fossil insects from the Albese Messinian (Piemonte) with a description of *Oryctodiplax gypsorum* n. gen. n. sp. (Odonata, Libellulidae)]. Bollettino della Società Paleontologica Italiana, 26(1-2): 151–176. (in Italian)
- CIESM (2008): The Messinian salinity crisis from mega-deposits to microbiology – A Consensus Report (No. 33 CIESM Workshop Monographs). – CIESM, Monaco, 168 pp.
- Charrier, G., Fernandez, D., Malaroda, R. (1964): La Formazione di Pianfolco (Bacino Oligocenico Ligure Piemontese) [The Pianfolco Formation (Oligocene Ligurian-Piemonte Basin)]. – Atti dell'Accademia Nazionale

dei Lincei, Memorie della Classe di Scienze Matematiche, Fisiche, Naturali, Serie 8, 7(2): 23-81. (in Italian)

- d'Atri, A., Irace, A., Piana, F., Tallone, S., Varrone, D., Bellino, L., Fioraso, G. Cadoppi, P., Fusetti, E., Morelli, M., Lanteri, L., Paro, L., Piccini, C., Trenkwalder, S., Violanti, D. (2016): Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 194, Acqui Terme [Explanatory notes of the Geological Map of Italy at scale 1:50,000, Sheet 194, Acqui Terme]. ISPRA, Roma, 229 pp. (in Italian)
- Dela Pierre, F., Bernardi, E., Cavagna, S., Clari, P., Gennari, R., Irace, A., Lozar, F., Lugli, S., Manzi, V., Natalicchio, M., Roveri, M., Violanti, D. (2011): The record of the Messinian salinity crisis in the Tertiary Piedmont Basin (NW Italy): The Alba section revisited. – Palaeogeography, Palaeoclimatology, Palaeoecology, 310: 238–255. https://doi.org/10.1016/j.palaeo.2011.07.017
- Dela Pierre, F., Clari, P., Bernardi, E., Natalicchio, M., Costa, E., Cavagna, S., Lozar, F., Lugli, S., Manzi, V., Roveri., M., Violanti, D. (2012): Messinian carbonate-rich beds of the Tertiary Piedmont Basin (NW Italy): microbially-mediated products straddling the onset of the salinity crisis. – Palaeogeography, Palaeoclimatology, Palaeoecology, 344: 78–93.
 - https://doi.org/10.1016/j.palaeo.2012.05.022
- Dela Pierre, F., Natalicchio, M., Lozar, F., Bonetto, S., Carnevale G., Cavagna S., Colombero S., Sabino M., Violanti, D. (2016). The northernmost record of the Messinian salinity crisis (Piedmont Basin, NW Italy). – Geological Field Trips, 8(2.1), 1–58.

https://doi.org/10.3301/GFT.2016.03

- Dela Pierre, F., Piana, F., Fioraso, G., Boano, P., Bicchi, E., Forno, M. G., Ruffini, R. (2003a): Carta Geologica d'Italia alla scala 1:50.000, Foglio 157 "Trino" [Geological Map of Italy scale 1:50,000, Sheet 157 'Trino']. – APAT, Agenzia per la Protezione dell'Ambiente e per i Servizi Tecnici, Dipartimento Difesa del Suolo, Roma, 1 map. (in Italian)
- Dela Pierre, F., Piana, F., Fioraso, G., Boano, P., Bicchi, E., Forno, M. G., Violanti, D., Clari, P., Polino, R. (2003b): Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 157 "Trino" [Explanatory notes of the Geological Map of Italy at scale 1:50,000, Sheet 157 'Trino']. – APAT, Agenzia per la Protezione dell'Ambiente e per i Servizi Tecnici. Dipartimento Difesa del Suolo, Roma, 147 pp. (in Italian)
- Denk, T. (2004): Revision of *Fagus* from the Cenozoic of Europe and southwestern Asia and its phylogenetic implications. Documenta naturae, 150: 1–72.
- Denk, T., Velitzelos, D., Güner, H. T., Bouchal, J. M., Grímsson, F., Grimm, G. (2017): Taxonomy and palaeoecology of two widespread western Eurasian Neogene sclerophyllous oak species: *Quercus drymeja* Unger and *Q. mediterranea* Unger. – Review of Palaeobotany and Palynology, 241: 98–128.

https://doi.org/10.1016/j.revpalbo.2017.01.005

- Dilcher, D. (1974): Approaches to the identification of angiosperm leaf remains. – The Botanical Review, 40(1): 1–145. https://doi.org/10.1007/BF02860067
- Ellis, B., Daly, D. C., Hickey, L. J., Johnson, K. R., Mitchell, J. D., Wilf, P., Wing, S. L. (2009): Manual of leaf

architecture. - New York Botanical Garden, New York, 190 pp.

https://doi.org/10.1079/9781845935849.0000

Frigerio, C., Bonadeo, L., Zerboni, A., Livio, F., Ferrario, M. F., Fioraso, G., Irace, A., Brunamonte, F., Michetti, A. M. (2017): First evidence for Late Pleistocene to Holocene earthquake surface faulting in the Eastern Monferrato Arc (Northern Italy): Geology, pedostratigraphy and structural study of the Pecetto di Valenza site. – Quaternary International, 451: 143–164. https://doi.org/10.1016/j.meint.2016.12.022

https://doi.org/10.1016/j.quaint.2016.12.022

- Gaudant, J. (1979): "Pachylebias" crassicaudus (Agassiz) (Poisson Téléostéen, cyprinodontiforme), un constituant majeur de l'ichthyofaune du Messinien continental du bassin méditerranéen. – Geobios 12: 47–73. https://doi.org/10.1016/S0016-6995(79)80108-4
- Gaudant, J., Courme-Rault, M. D., Fornaciari, E., Fourtanier, E. (2010): The Upper Miocene fossil fish locality of Pecetto di Valenza (Piedmont, Italy): A multidisciplinary approach. – Bollettino della Società Paleontologica Italiana, 49(3): 203–225.
- Güner, T. H., Bouchal, J. M., Köse, N., Göktas, F., Mayda, S., Denk, T. (2017): Landscape heterogeneity in the Yatağan Basin (southwestern Turkey) during the middle Miocene inferred from plant macrofossils. – Palaeontographica, Abt. B, 296(1-6): 113–171. https://doi.org/10.1127/palb/296/2017/113
- Hably, L. (2010): The Early Oligocene flora of Santa Giustina (Liguria, Italy) – Revision and comparison with the flora of Tard Clay Formation. – Rivista Italiana di Paleontologia e Stratigrafia, 116(3): 405–420.
- Heer, O. von. (1853): Über die vorweltliche Flora der Schweiz. Gartenflora, 2: 289–297.
- Heer, O. von. (1859): Die tertiäre Flora der Schweiz. 3. Wurster, Winterthur, 200 pp.
- Irace, A., Catanzariti, R., Fioraso, G., Da Prato, S., Barbero, E., Bonadeo, L., Livio, F., Ferrario, F., Scaramuzzo, E., Zerboni, A. (2022): Geological map of Valenza-Montecastello area: New field constraints for the Oligocene-Quaternary tectono-stratigraphic evolution of the eastern Monferrato (NW Italy). In: Carmina, B., Fascio, L., Innamorati, G., Pasero, M., Petti F. M. (eds), Abstract book, SGI-SIMP Congress, September 19th–21st 2022, Torino, Italy, p. 895.
- Irace, A., Clemente, P., Piana, F., De Luca, D. A., Polino, R., Violanti, D., Mosca, P., Trenkwalder, S., Natalicchio, M., Ossella, L., Governa, M., Petricig, M. (2010a): Hydrostratigraphy of the late Messinian-Quaternary basins in the southern Piedmont (northwestern Italy). – Memorie descrittive della Carta Geologica d'Italia, 90: 133–152.
- Irace, A., Dela Pierre, F., Rossi, M., Rogledi, S., Piana, F. (2010b): The Messinian deposits of the Alto Monferrato (Southern Tertiary Piedmont Basin): Evidences of a margin-basin transition zone during the Messinian Salinity Crisis. In: Bertok, C., d'Atri, A., Martire, L., Perotti, E. (eds), Abstract book, Geosed Congress, September 19th–25th 2010, Torino, Italy, pp. 38–39.
- Jähnichen, H., Mai, D. H., Walther, H. (1980): Blätter und Früchte von *Cercidiphyllum* Siebold & Zuccarini im mitteleuropäischen Tertiär. – Schriftenreihe für Geologische Wissenschaften, 16: 357–399.

Kvaček, Z., Hurník, S. (2000): Revision of Early Miocene plants preserved in baked rocks in the North Bohemian Tertiary. – Acta Musei Nationalis Pragae, Series B, Historia Naturalis, 56: 1–48.

https://doi.org/10.14446/AMNP.2015.55

- Kvaček, Z., Teodoridis, V., Denk, T. (2020): The Pliocene flora of Frankfurt am Main, Germany: Taxonomy, palaeoenvironments and biogeographic affinities. – Palaeobiodiversity and Palaeoenvironments, 100(3): 647–703. https://doi.org/10.1007/s12549-019-00391-6
- Kvaček, Z., Teodoridis, V., Roiron, P. (2011): A forgotten Miocene mastixioid flora of Arjuzanx (Landes, SW France). – Palaeontographica, Abt. B, 285: 3–111. https://doi.org/10.1127/palb/285/2011/3
- Kvaček, Z., Velitzelos, D., Velitzelos, E. (2002): Late Miocene flora of Vegora, Macedonia, N. Greece. – University of Athens, Athens, 175 pp.
- Ludwig, R. (1860): Fossile Pflanzen aus der ältesten Abteil der Rhein-Wetterauer Tertiärformation. – Palaeontographica, 8: 137–154.
- Macaluso, L., Martinetto, E., Vigna, B., Bertini, A., Cilia, A., Teodoridis, V., Kvaček, Z. (2018): Palaeofloral and stratigraphic context of a new fossil forest from the Pliocene of NW Italy. – Review of Palaeobotany and Palynology, 248: 15–33.
 - https://doi.org/10.1016/j.revpalbo.2017.08.005
- Martinetto, E. (2003): Leaves of terrestrial plants from the shallow marine and transitional Pliocene deposits of Asti (Piedmont, NW Italy). Bollettino della Società Paleon-tologica Italiana, 42: 11–75.
- Martinetto, E. (2011): The first mastixioid fossil from Italy and its palaeobiogeographic implications. – Review of Palaeobotany and Palynology, 167: 222–229. https://doi.org/10.1016/j.revpalbo.2011.08.004
- Martinetto, E. (2015): Monographing the Pliocene and Early Pleistocene carpofloras of Italy: Methodological challenges and current progress. Palaeontographica, Abt. B, 293: 57–99.

https://doi.org/10.1127/palb/293/2015/57

- Martinetto, E., Bertini, A., Mantzouka, D., Natalicchio, M., Niccolini, G., Kovar-Eder, J. (2022): Remains of a subtropical humid forest in a Messinian evaporite-bearing succession at Govone, northwestern Italy – Preliminary results. – Fossil Imprint, 78(1): 157–188. https://doi.org/10.37520/fi.2022.007
- Martinetto, E., Bicchi, E., Cavallo, O., Damarco, P., Dela Pierre, F., Fassio, A., Imbriano, F., Lozar, F., Natalicchio, M., Pane, V., Repetto, G. (2023): Macrofossili di piante terrestri da siti neogenici del Piemonte meridionale. – Rivista piemontese di Storia naturale, 44: 17–62.
- Martinetto, E., Rista, C., Tarabra, E. (2000): Classificazione e ordinamento museologico di foglie di Angiosperme messiniane dell'Albese [Classification and museological sorting of leaves of Messinian Angiosperms from the Albese area]. – Alba Pompeia, N. S., 21(1): 3–30. (in Italian)
- Martinetto, E., Uhl, D., Tarabra, E. (2007): Leaf physiognomic indications for a moist warm-temperate climate in NW Italy during the Messinian (Late Miocene). – Palaeogeography, Palaeoclimatology, Palaeoecology, 253: 41–55.

https://doi.org/10.1016/j.palaeo.2007.03.033

- Niccolini, G., Bertini, A., Lanini, B., Menichetti, E., Fusco, F., Hakobyan, E., Martinetto, E., (2022): Late Messinian flora from the post-evaporitic deposits of the Piedmont Basin (NW, Italy). – Fossil Imprint, 78: 189–216. https://doi.org/10.37520/fi.2022.008
- Parenti, L. (1981): A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). Bulletin of the American Museum of Natural History, 168: 335–557.
- Patterson, C., Rosen, D. E. (1977): Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. – Bulletin of the American Museum of Natural History, 158: 83–172.
- Pavia, G. (1989): Il giacimento a pesci messiniani di Pecetto di Valenza (Alessandria) [The Messinian fish deposit of Pecetto di Valenza (Alessandria)]. – Bollettino della Società Piemontese di Archeologia e Belle Arti, 43: 15–21. (in Italian)
- Pellegrino, L., Abe, K., Gennari, R., Lozar, F., Dela Pierre, F., Natalicchio, M., Mikami, Y., Jordan, R. W., Carnevale, G. (2020a): Integrated micropaleontological study of the Messinian diatomaceous deposits of the Monferrato Arc (Piedmont basin, NW Italy): New insights into the paleoceanographic evolution of the northernmost Mediterranean region. – Marine Micropaleontology, 160: 101910 (19 pp.).

https://doi.org/10.1016/j.marmicro.2020.101910

- Pellegrino, L., Dela Pierre, F., Jordan, R. W., Abe, K., Mikami, Y., Natalicchio, M., Gennari, R., Lozar, F., Carnevale, G. (2020b): The upper Miocene diatomaceous sediments of the northernmost Mediterranean region: A lamina-scale investigation of an overlooked palaeoceanographic archive. – Sedimentology, 67: 3389–3421. https://doi.org/10.1111/sed.12748
- Peola, P. (1899): Florula messiniana di Monte Castello d'Alessandria. – Bollettino della Società Geologica Italiana, 18: 44–51.
- Peola, P. (1900a): Flora tongriana di Pavone d'Alessandria. – Bollettino della Società Geologica Italiana, 19: 36–62.
- Peola, P. (1900b): Flora del Tongriano di Bagnasco e Nucetto. – Rivista Italiana di Paleontologia, 6(2): 79–88.
- Peola, P. (unpublished [about 1899]): Flora terziaria del Piemonte [Tertiary flora of Piemonte]; unpublished monograph. – MS, 263 pp. (in Italian) (copy in the Malaroda Library of the Università degli Studi di Torino, Italy)
- Piana, F., Barale, L., Compagnoni, R., d'Atri, A., Fioraso, G., Irace, A., Mosca, P., Tallone, S., Monegato, G., Morelli, M. (2017a): Geological map of Piemonte region at 1:250,000 scale. Explanatory Notes. – Accademia delle Scienze di Torino, Memorie Scienze Fisiche, 41: 1–143. https://doi.org/10.1080/17445647.2017.1316218
- Piana, F., Fioraso, G., Irace, A., Mosca, P., d'Atri, A., Barale, L., Falletti, P., Monegato, G., Morelli, M., Tallone, S., Vigna, G. B. (2017b): Geology of Piemonte region (NW Italy, Alps-Apennines interference zone). – Journal of Maps, 13(2): 395–405.
- Reichenbacher, B., Kowalke, T. (2009): Neogene and present-day zoogeography of killifishes (*Aphanius* and *Aphanolebias*) in the Mediterranean and Paratethys areas. –

Palaeogeography, Palaeoclimatology, Palaeoecology, 281: 43–56.

https://doi.org/10.1016/j.palaeo.2009.07.008

Sacco, F. (1890): Il bacino terziario e quaternario del Piemonte [The Tertiary and Quaternary basin of Piemonte]. –Tip[ografia] Bernardoni di C. Rebeschini e C., Milano, 643 pp. (in Italian)

https://doi.org/10.5962/bhl.title.161246

- Saporta, G. D., Marion, A. F., Falsan, A. (1872): Recherches sur les végétaux fossiles de Meximieux, précédées d'une introduction stratigraphique. – Archives du Muséum d'histoire naturelle de Lyon, 1(1): 131–335. https://doi.org/10.3406/mhnly.1872.937
- Sordelli, F. (1896): Studi sulla vegetazione di Lombardia durante i tempi geologici [Studies on the vegetation of Lombardy during geological times]. – Tipografia L. F. Cogliati, Milano, 300 pp. (in Italian) https://doi.org/10.5962/bbl.title.134650

https://doi.org/10.5962/bhl.title.134650

- Sturani, C., Sampo, M. (1973): Il Messiniano inferiore in facies diatomitica nel Bacino terziario Piemontese [The Lower Messinian in diatomitic facies in the Tertiary Piemonte Basin]. – Memorie della Società Geologica Italiana, 12: 335–358. (in Italian)
- Srivastava, G., Su, T., Mehrotra, R. C., Kumari, P., Shankar, U. (2019): Bamboo fossils from Oligo-Pliocene sediments of northeast India with implications on their evolutionary ecology and biogeography in Asia. – Review of Palaeobotany and Palynology, 262: 17–27. https://doi.org/10.1016/j.revpalbo.2018.12.002
- Teodoridis, V., Kvaček, Z., Sami, M., Utescher, T., Martinetto, E. (2015): Palaeoenvironmental analysis of the Messinian macrofossil floras of Tossignano and Monte Tondo (Vena del Gesso basin, Romagna Apennines, northern Italy). Acta Musei Nationalis Pragae, Series B, Historia Naturalis, 71(3-4): 249–292. https://doi.org/10.14446/AMNP.2015.249
- Teodoridis, V., Kvaček, Z., Sami, M. (2017): Revision of the Messinian flora of Polenta (Romagna Apennines, North-

ern Italy). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 283: 221–237. https://doi.org/10.1127/njgpa/2017/0638

- Vannucci, G., Piazza, M., Fravega, P., Chiesa, I. (1994): Calcareous Rhodophyceae from the "Astian facies" (Pliocene), Valle San Bartolomeo, Alessandria, MW Italy. – Bollettino della Società Paleontologica Italiana, 3: 351–364.
- Vasilyan, D., Reichenbacher, B., Carnevale, G. (2009): A new fossil *Aphanius* species from the Upper Miocene of Armenia (Eastern Paratethys). – Paläontologische Zeitschrift, 83: 511–519. https://doi.org/10.1007/s12542-009-0034-4

Velitzelos, D. (ed.) (2002): Field guide to the Neogene of the Island of Evia – Early Miocene flora of Kymi. – University of Athens, Athens, 61 pp. http://doi.org/10.13140/2.1.1180.1925

- Wang, L., Jacques, F. M. B., Su, T., Xing, Y. W., Zhang, S. T., Zhou, Z. K. (2013): The earliest fossil bamboos of China (middle Miocene, Yunnan) and their biogeographical importance. – Review of Palaeobotany and Palynology, 197: 253–265. https://doi.org/10.1016/j.revpalbo.2013.06.004
- Wang, Q., Ma, F., Yang, Y., Dong, J., Wang, H., Li, R., Xu, X., Sun, B. N. (2014): Bamboo leaf and pollen fossils from the late Miocene of eastern Zhejiang, China and their phytogeographical significance. – Acta Geologica Sinica, 88: 1066–1083. https://doi.org/10.1111/1755-6724.12274
- Worobiec, E., Worobiec, G. (2005): Leaves and pollen of bamboos from the Polish Neogene. – Review of Palaeobotany and Palynology, 133(1-2): 39–50. https://doi.org/10.1016/j.revpalbo.2004.08.004
- Zidianakis, G., Iliopoulos, G., Zelilidis, A., Kovar-Eder, J. (2020): Three (middle to) late Miocene plant macroremain assemblages (Pitsidia, Kassanoi and Metochia) from the Messara-Gavdos region, southern Crete. – Acta Palaeobotanica, 60(2): 333–437.
 - https://doi.org/10.35535/acpa-2020-0018