Drainage network geometry versus tectonics in the Argentera Massif (French–Italian Alps)

Adriano Ribolini, Matteo Spagnolo*

Dipartimento di Scienze della Terra, Università di Pisa, PISA, Italy

Received 8 May 2006; received in revised form 26 February 2007; accepted 26 February 2007
Available online 6 March 2007

Abstract

The Argentera Massif (French–Italian Alps), with its uniform lithology, was selected to evaluate how known Plio–Pleistocene tectonics have conditioned the drainage network geometry. The drainage network was automatically derived and ordered from a 10 m-resolution DEM. On hillshade images, alignments of morphological features were identified. The Massif was subdivided into 22 domains of 50 km² within which the directions of every river channel segment and the direction of the aligned morphological features were compared and contrasted with the strike of tectonic structures measured in the field. Results suggest that the Argentera drainage system is variously controlled by recent tectonics, depending on the Massif sector taken into account. In the NW sector, the vertical uplift is less because the strain has been accommodated in an oblique direction along a lateral thrust. In the SE sector, strain in a predominantly vertical direction along a frontal thrust has resulted in a major vertical displacement. Accordingly, the NW sector is characterized by (i) a strong geometric relationship between the main tectonic structures and the directions of river channels, (ii) longitudinal main rivers bordering the Massif, and (iii) a general trellis pattern within the domains. In the SE sector, the prolonged uplift has forced an original longitudinal drainage system to develop as a transverse system. This change has occurred by means of fluvial captures that have been identified by the presence of windgaps, fluvial elbows and knickpoints. At the domain scale, intense uplift of the SE sector has prompted the drainage pattern to evolve as a dendritic type with no clear influence of structure in the channel orientations.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Drainage network pattern; Channel orientation; Tectonic geomorphology; Remote sensing; Argentera Massif

1. Introduction

In tectonically active mountain regions, the drainage network reflects the interaction between surface processes and the growth and propagation of the thrust faults and folds that have led to the formation of an orogen (Jackson and Leeder, 1994; Delcaillau et al., 1998; Alvarez, 1999; Burbank and Anderson, 2001; Schlunegger and Hinderer, 2001; van der Beek et al., 2002; Delcaillau et al., 2006). Field-based investigations, laboratory experiments and numerical models have shown that variation in the style of bedrock deformation, due to rock uplift, causes perturbations in the fluvial network (Ouchi, 1985; Burbank, 1992; Gupta 1997; Mueller and Talling, 1997; Jackson et al., 1998; Hasbargen and Paola 2000; Hallet and Molnar, 2001; Pelletier, 2004; Vetel et al., 2004; Ghassemi, 2005).

Several 2- and 3-D channel indices have been used to prove the strong sensitivity of the fluvial system to active tectonics (Abrahams and Flint, 1983; Seeber and...
events that have occurred in a mountain range. Can be used as a tool for reconstructing the deformative relationship between channel orientation and structures tectonics evolution, can provide new insights on how the and uplift. This work, carried out in an area of known Argentera Massif and (ii) how this relationship can be main thrust fault systems in different sectors of the between the geometry of the drainage network and the and is elongated from SE to NW. The Gesso and Stura valleys in Italy, together with the Tinée and Vesubié valleys in France, are the main fluvial systems of the Massif (Fig. 1). The climate of the Massif is highly variable depending on altitude and valley aspect. Climatic data from a central area near the Cima dell’Argentera (Lago del Chiotas station at 2000 m asl) show a mean annual air temperature of 4.0 °C, while mean annual rainfall is about 1000 mm (Rapetti and Vittorini, 1992).

The Argentera Massif is made up of metamorphic (high-grade schists and migmatites) and granitoid rocks of the European Variscan basement (Fry, 1989; Bogdanoff et al., 1991 and references therein) (Fig. 1). Permian to Cenozoic sediments have been partly detached from the basement at the level of the Triassic evaporites and they outcrop all around the crystalline Massif (Malaroda et al., 1970; Siddans, 1980; Musumeci and Colombo, 2002; Delteil et al., 2003).

The Alpine structures cross-cutting the basement are represented mainly by shear zones, strike-slip and reverse faults, often reactivating pre-Alpine (Variscan) structures (Bortolami, 1970; Malaroda et al., 1970; Malaroda, 1974; Bogdanoff, 1986; Bogdanoff et al., 1991; Musumeci et al., 2003). The Bersezio-Colle della Lombarda (BCL) and the Fremamorta-Colle del Sabione (FCS) fault systems are the main tectonic structures in the NW and SE sectors of the Massif respectively (Fig. 1). They are both interpreted as high-angle shear zones, along which micaschists and mylonitic rocks crop out. In the NW sector a right-lateral component is described for the faults associated with the BCL system (Horrenberger et al., 1978), and in the SE sector a reverse mechanism dominates the FCS structures (Musumeci et al., 2003). The NW sector is characterized by a dense set of faults that strike NW–SE and are related to the BCL, while the main tectonic elements of the SE sector show a WNW–ESE orientation connected to the FCS (Fig. 1).

These structural features result from the superimposition of two main deformative events that occurred during the Alpine tectonics (Bogdanoff, 1986). During the most recent event (Upper Miocene–Pliocene), the NE portion of the Argentera was thrust onto the rest of the Massif toward the SW. This thrusting occurred along the FCS and was kinematically linked to dextral strike-slip along the BCL, which acted as a steep lateral ramp.

2. Regional setting

The Argentera Massif is located in the southernmost Western European Alps, known as the Maritime Alps. The Massif outcrop covers an area of about 1000 km² and is elongated from SE to NW. The Gesso and Stura valleys in Italy, together with the Tinée and Vesubié valleys in France, are the main fluvial systems of the Massif (Fig. 1). The climate of the Massif is highly variable depending on altitude and valley aspect. Climatic data from a central area near the Cima dell’Argentera (Lago del Chiotas station at 2000 m asl) show a mean annual air temperature of 4.0 °C, while mean annual rainfall is about 1000 mm (Rapetti and Vittorini, 1992).

The Argentera Massif is made up of metamorphic (high-grade schists and migmatites) and granitoid rocks of the European Variscan basement (Fry, 1989; Bogdanoff et al., 1991 and references therein) (Fig. 1). Permian to Cenozoic sediments have been partly detached from the basement at the level of the Triassic evaporites and they outcrop all around the crystalline Massif (Malaroda et al., 1970; Siddans, 1980; Musumeci and Colombo, 2002; Delteil et al., 2003).

The Alpine structures cross-cutting the basement are represented mainly by shear zones, strike-slip and reverse faults, often reactivating pre-Alpine (Variscan) structures (Bortolami, 1970; Malaroda et al., 1970; Malaroda, 1974; Bogdanoff, 1986; Bogdanoff et al., 1991; Musumeci et al., 2003). The Bersezio-Colle della Lombarda (BCL) and the Fremamorta-Colle del Sabione (FCS) fault systems are the main tectonic structures in the NW and SE sectors of the Massif respectively (Fig. 1). They are both interpreted as high-angle shear zones, along which micaschists and mylonitic rocks crop out. In the NW sector a right-lateral component is described for the faults associated with the BCL system (Horrenberger et al., 1978), and in the SE sector a reverse mechanism dominates the FCS structures (Musumeci et al., 2003). The NW sector is characterized by a dense set of faults that strike NW–SE and are related to the BCL, while the main tectonic elements of the SE sector show a WNW–ESE orientation connected to the FCS (Fig. 1).

These structural features result from the superimposition of two main deformative events that occurred during the Alpine tectonics (Bogdanoff, 1986). During the most recent event (Upper Miocene–Pliocene), the NE portion of the Argentera was thrust onto the rest of the Massif toward the SW. This thrusting occurred along the FCS and was kinematically linked to dextral strike-slip along the BCL, which acted as a steep lateral ramp.
transpressive transcurrent fault). NW–SE striking thrust surfaces border the Massif both at the SE and N margins, while a right-lateral shear zone cross-cuts NE Argentera. All these bordering structures accommodated the NW–SE crustal shortening, which built a pop-up structure.

Although a slight glacier-induced isostatic rebound cannot be neglected, tectonic forcing can be considered as the principal cause of the recent uplift and exhumation of the Argentera (Debelmas, 1986; Bigot-Cormier, 2002). Seismic and GPS data document that the area is tectonically active, with crustal shortening of 2–4 mm yr\(^{-1}\) induced by N–S to NE–SW compression (Frechet and Pavoni, 1979; Madeddu et al., 1996; Calais et al., 2000).

Exhumation of the Massif began between the Late Oligocene and early Miocene, and underwent an increase at 3.5 Ma to rates of 0.8–1 mm yr\(^{-1}\) (Bigot-Cormier et al., 2000; Bogdanoff et al., 2000; Bigot-Cormier, 2002). The crystalline basement started to be eroded only from Late Miocene times (Iaworsky and Curti, 1960).

Apatite fission track analysis shows variable denudation rates that have been interpreted in terms of differential vertical uplift of crustal blocks (Bogdanoff et al., 2000; Bigot-Cormier, 2002). This spatial variation in denudation and uplift is also shown by the overall morphology of the Massif (Ribolini, 1998; Ribolini, 2000; Musumeci et al., 2003). In particular, due to the SW vergence of thrusting, the Massif presents an overall asymmetry, with the NE side much wider, with longer and wider basins and a more developed drainage hierarchy than the SW side. The SE portion of the Massif, characterized by the highest elevations (>3000 m), relief and drainage density, is thought to be the area that has experienced the highest rate of Late Alpine and active tectonic uplift (Musumeci et al., 2003).

3. Materials and methods

The drainage network of the Argentera Massif was automatically derived from a 10 m-resolution DEM. We applied the GIS flow accumulation method (Jenson and Dominique, 1988) with a threshold of 400 m\(^2\). Morphologically, the derived network includes all ephemeral channels that usually have running water during the
wet seasons and that occasionally become debris flow or avalanche channels.

We investigated the drainage network of the Argentera Massif as follows. In one case, together with the general geometry of the channels of Horton–Strahler order equal or higher than 3, we looked at the presence of knickpoints along river profiles in relation to windgaps. In a second case, we subdivided the Massif
into domains of 50 km² and within each domain we focused on the directional properties of (i) every channel from the 1st to the 6th order, and (ii) other linear morphological features.

With specific GIS tools, we evaluated the direction and length of every digitized segment (between two vertexes) within every channel of the drainage network. In total we analyzed 27,821 segments of 5761 channels (Fig. 2a).

Rectilinear valleys, valley walls, ridges, crests, passes or a combination of these features, when aligned, were drawn as lines at two different scales (1:50,000 and 1:100,000) on four DEM-derived hillshade images with different light source orientation. Although these lines correspond to “lineaments” sensu Wise et al. (1985), this term is not used here to avoid possible misinterpretation with structural lineaments. In this paper the word “lineament” will be used only when aligned features have been proved to correspond to the intersection between the surface and the main fault and fracture systems. Only aligned features that were recognized independently by both authors were taken into account (Fig. 2b). Direction and length were quantified for each of the 464 selected aligned features. The correspondence between the remote sensing-derived aligned features and the geological structures of the area was verified by means of several geological field surveys.

Each domain of 50 km² is large enough to include more than one valley or drainage basin of the 4th order, and at least 10 aligned morphological features. On average, each domain includes 3.9 basins of 4th order, 1.7 basins of 5th order and 31 aligned features. For the sake of lithological uniformity, we considered only domains where at least 50% of the area is covered by a crystalline rock outcrop (Fig. 2). For each of the 22 domains that were found in the crystalline rocks, a length-weighted frequency rose diagram with angular intervals of 10° was created for both the drainage network and the aligned features analysis. With the aim of identifying only those domains where the drainage network shows a clear preferred orientation, an 11% frequency threshold was applied to the direction analysis results. The 11% threshold, although somehow subjective, was chosen here as it corresponds to twice the theoretical value (5.5%) of a perfectly homogeneous frequency distribution in all 18 angular intervals of 10° (100/18 = 5.5).

4. Results

4.1. Regional analysis of the drainage network

Examining only the higher order channels (5th and 6th orders), the Massif is drained by four main rivers: the
Table 1

<table>
<thead>
<tr>
<th>Name</th>
<th>Mean elevation (in metres asl)</th>
<th>Mean slope (in degrees)</th>
<th>Area (in square kilometres)</th>
<th>Drainage density (1/km²)</th>
<th>Code</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tinée</td>
<td>1900</td>
<td>29.56</td>
<td>287</td>
<td>2.65</td>
<td>A</td>
</tr>
<tr>
<td>Vésubie</td>
<td>2029</td>
<td>29.08</td>
<td>178</td>
<td>2.80</td>
<td>B</td>
</tr>
<tr>
<td>Stura</td>
<td>1989</td>
<td>32.59</td>
<td>259</td>
<td>3.55</td>
<td>C</td>
</tr>
<tr>
<td>Gesso</td>
<td>1979</td>
<td>35.13</td>
<td>276</td>
<td>3.20</td>
<td>D</td>
</tr>
<tr>
<td>Boréon</td>
<td>2193</td>
<td>29.15</td>
<td>38</td>
<td>2.82</td>
<td>I</td>
</tr>
<tr>
<td>Mollières</td>
<td>2222</td>
<td>24.27</td>
<td>31</td>
<td>2.65</td>
<td>2</td>
</tr>
<tr>
<td>Chastillon</td>
<td>2226</td>
<td>25.31</td>
<td>22</td>
<td>2.36</td>
<td>3</td>
</tr>
<tr>
<td>Orgials</td>
<td>2237</td>
<td>25.00</td>
<td>9</td>
<td>2.33</td>
<td>4</td>
</tr>
</tbody>
</table>

The profiles into two portions. The gradient of the portion of the profiles downstream of the knickpoints varies in the four rivers. In particular, the lowest gradient (8%) is found in the Boréon river profile, an intermediate value (11%) in the Mollières profile and the highest values in the Chastillon and Orgials profiles (around 13%). Thus, a trend of increasing gradients from the SE to the NW rivers is observed. Analogously, both mean slope and drainage density of the four corresponding basins tend to decrease moving from the SE to the NW basins (Table 1).

4.2. Domain analysis of drainage network

Of the 22 domains analyzed, there are 9 whose drainage network shows a preferred orientation with a frequency higher than the 11% threshold. Domains 5, 6, 9, 10, 16, 21 are in the NW sector of the Massif, while the remaining three domains (19, 23, 25) are in the SE sector (Fig. 5a).

The drainage networks within domains 6, 9, 16, 21, 23 and 25 all show a dominant NE–SW direction. In particular within domains 6 and 9 the network has a typical trellis pattern with one main stem that flows from NW to SE bordering the Massif (the Stura and Tinée rivers, respectively) and several perpendicular tributaries. A similar organization can be found within domains 16 and 21, with tributaries more or less perpendicular to the main Tinée River.

In domains 5, 10 and 19 the drainage network shows a preferred NW–SE orientation. In particular, in domains 5 and 10 the most frequent drainage direction corresponds to several 1st, 2nd or even 3rd order channels, tributaries of the main 4th order valleys flowing from SW to NE. Their drainage network exhibits a typical trellis pattern.

4.3. Domain analysis of aligned morphological features and geological field data

We focus on the 9 domains that exhibit a clear drainage orientation (5, 6, 9, 10, 16, 19, 21, 23, 25). In these domains, the most frequent directions of the feature alignments can be clustered as follows: 140–150°N, with a frequency of almost 14%, 110–120°N (10%) and 50–60°N (6%) (Fig. 5b). In the NW sector of the Massif, domains 5, 6, 9, and 10 are characterized by a frequent direction of 140–150°N. In domains 19, 23 and 25 (SE sector) most aligned features are found in the 110–130°N interval.

Geological field surveys have shown that aligned valleys, scarps, saddles and crests largely correspond to narrow zones of intensely faulted and fractured rocks.
Fault and fracture strikes are consistent with the directions of the feature alignments that, from now on, will be referred to as lineaments. In particular, NW-sector domains 5, 6, 10 are dominated by fault planes striking NW–SE (130°–140°N) and moderately- to steeply-dipping towards NE, all related to the BCL shear zone.

Fig. 4. Sketch map of the present-day Boréon, Mollières, Chastillon and Orgials rivers and crest line, windgaps are showed as reversed brackets (a). Topographic profiles along the divide between Boréon and Mollières (a), Mollières and Chastillon (b) and Chastillon and Orgials (c) basins; location and interval of the profiles are shown in the sketch map. Longitudinal river profiles of the four rivers, black arrows show the knickpoints (c).
Kinematic indicators show a SW reverse movement, with a component of right-lateral slip. In the SE-sector domains 19 and 25, several NW–SE (110–120°N) fault planes were identified, whose slickenside striae and kinematic indicators show a SSW reverse sense of movement. These faults are the expression of the FCS south-facing thrust
(foliation planes 100–110°N, dipping 60–70°N) and related backthrust (foliation planes 110–120°N, dipping 60–70°S).

5. Discussion

5.1. Drainage network directions and lineaments

Within the 9 selected domains where a clear drainage orientation is found, two main types of geometric relationship between drainage network and lineaments exist.

The “A-type” (Fig. 7) refers to domains where the main orientation of the drainage network is the same as the lineaments. A typical example is that of domain 5 in the NE sector of the Massif (Figs. 5 and 6). Here, identified lineaments and geological surveys indicate the presence of a wide band of strike-slip faults with a NW–SE orientation. These faults crosscut the three main rivers of domain 5 that flow E–W or SW–NE.
Most tributaries of these main rivers (usually 1st and 2nd order channels) are NW–SE elongated, determining the high frequency of this direction in the drainage orientation analysis.

The “B-type” occurs where the most frequent drainage direction is given by the orientation of several low order channels that run perpendicular to the main river stem and to the lineaments (Fig. 7). The B-type typically occurs in the bordering domains, especially in the NW sector along the Tinée and the Stura rivers. An example is domain 9 (Figs. 5 and 6), where the 6th order Tinée River runs from NW to SE along a major fault that borders the Massif. Several 3rd and 4th order channels join the main Tinée River perpendicularly. The main lineament direction found in this domain is NW–SE.

Overall, domains where there is a clear direct (A-type) and indirect (B-type) relationship between the drainage network and the lineaments are mostly concentrated in the NW sector of the Argentera Massif.

5.2. Drainage network pattern and tectonics

5.2.1. SE sector of the Massif

In this sector we considered the largest left tributaries of the Tinée River (Chastillon and Mollières basins) together with the upper Vesubié River Basin (SW side of the Massif) and the Orgiols and Gesso River basins (NE side). In this sector most faults are related to the FCS thrust system. Along this system, Neogene strain is accommodated in a prevalently vertical direction, determining the highest rate of exhumation and uplift within the Massif. As to be expected in an area characterized by an intense vertical movement and consequent high relief, the drainage network has become typically dendritic (Fig. 2a) and does not show any particular directional trend. This is why in this sector of the Massif, there is a lack of preferred orientation of the drainage within the domains (Fig. 5). Moreover, in the only 3 cases where a preferred orientation was found (domains 19, 23, 25), there is no clear

Fig. 7. Two different types (A-type and B-type) of relationship between lineaments and channel directions.
correspondence between preferred direction of the drainage network and strike of lineaments (nor A- or B-type geometric relationships).

Both the Gesso and Vesubié rivers show the characteristics of trans-orogenic drainage systems: the highest hierarchical ordered channels are oriented parallel to the crustal shortening direction, crossing the main geological structures at right angles.

5.2.2. NW sector of the Massif

In the NW sector we included the left-bank tributaries of the upper Tinée River (SW side of the Massif) and the right-bank tributaries of the upper Stura River (NE side). This sector is characterized by the presence of transcurrent faults, most of them related to the BCL shear zone. During Neogene thrusting, strain was accommodated along a prevalently oblique direction in this sector, with the BCL system acting as a lateral ramp. The consequent limited vertical uplift has not created the high relief conditions present in the SE sector. The lower relief of the NW sector results in a generally higher sensitivity of the drainage network to fault and fracture systems, thus determining the general trellis pattern (Fig. 2a) and the high concentration of domains with an oriented drainage network (Fig. 5) usually related to the main geological structures. In particular, near the main Stura and Tinée valleys, domains are characterized by a drainage network that shows a preferred orientation perpendicular to the main direction of the lineaments (Fig. 5), corresponding to the orientation of bordering faults (B-type domains). Conversely, a direct relationship between the preferred orientation of the geological structures and the drainage network occurs in the inner area of the SE sector (Fig. 5). In this case, the belt of densely faulted rocks related to the BCL shear zone conditions the development of several low order channels (A-type domains).

In the NW sector, the Tinée and Stura main rivers show the characteristics of an intra-orogenic drainage system, flowing longitudinally from NW to SE, following the strike of known geological structures (Horrenberger et al., 1978; Follacci et al., 1984; Guardia and Ivaldi, 1985). Once approaching the SE sector, the two rivers diverge from their longitudinal aspect and move away from the Massif due to the higher uplift that characterizes the SE sector. Coherently, in the area where the two rivers diverge the presence of thrust faults has been documented (Perello et al., 2001; Delteil et al., 2003).

5.3. Evidence of a paleo-river in the present-day drainage network

The adjacent 4th order Boréon, Mollières, Chastillon and Orgials rivers are aligned along a NW–SE direction (Fig. 3), following the strike of the southern prolongation of the BCL (Figs. 1 and 4). Windgaps are found along the divide between each two adjacent valleys at the intersection with the BCL (Fig. 4b). Their common orientation, together with the presence of the windgaps, suggests that all these rivers were once part of a single longitudinal intra-orogenic main river, parallel to the present-day upper Tinée and Stura rivers. The right side of the corresponding paleo-valley was the hanging wall of the BCL transpressive fault (Fig. 8).

The presence of fluvial elbows and knickpoints in a same river is usually a good indicator of a fluvial capture (e.g. Bishop, 1995 and references therein). In each of the 4 rivers analyzed both elements were found close to one another and also not far from the windgaps (Fig. 4a), thus allowing us to infer that the fluvial reorganization occurred by means of four fluvial captures. At some time during the mountain range growth and progressive exhumation, the original longitudinal paleo-river became a hanging river with respect to the transverse left-bank tributaries of the Tinée River. These channels, because of an increase in their gradient caused by the uplift, retreated backward and intercepted the hanging river, thus causing the fluvial captures. This determined the formation of the fluvial elbows and windgaps that are still evident. Moreover, each captured portion of the longitudinal river experienced a lowering of the base level, which in turn caused the formation of the still recognizable knickpoints (Fig. 4c). The overall result of this fluvial reorganization is a shift from a longitudinal to a transverse river system, as similarly documented in nearby Alpine regions (Federici and Malaroda, 2006) and in other thrust/fold mountain ranges (Jones, 2004; Delcaillau, 2006).

The timing of the four captures can be identified by linking both geological and morphological data. Apatite fission track analysis indicates that the SE sector of the Massif underwent a more intense uplift starting from 3.5 Ma (Bigot-Cormier, 2002) with respect to the NW sector. Therefore, it is likely that the transverse channels, whose erosive power was increasing in relationship with the uplift, were able to capture the longitudinal river first in the SE sector. The Boréon, Mollières, Chastillon and Orgials longitudinal profiles downhill of the knickpoints show a progressively steeper gradient while moving from the SE to the NW rivers. This suggests that the SE rivers had relatively more time to adjust to the lowering of the base level caused by the capture than the NW rivers, indicating again that the captures happened first in the SE sector. Consistently, in the Boréon basin the erosive processes that followed the base level lowering had the time to develop a larger drainage network (drainage
density) and steeper valley flanks (mean slope) with respect to the NW basins (Table 1).

6. Conclusions

The Argentera drainage system is differentially controlled by the active tectonic evolution of the area, depending on the Massif sector that is taken into account. Basement rocks of the NW sector have undergone less vertical displacement because the strain is accommodated in a prevalent oblique direction. As a consequence, the influence of selective erosion on the development of the channel orientation is still intense: (i) most channels are directly (A-type) or indirectly (B-type) related to the lineaments, (ii) the pattern of the drainage network is trellis, and (iii) the main rivers flow longitudinally to the Massif.

In the SE sector, vertical uplift is more intense than in the NW sector because the strain is accommodated in a predominantly vertical direction. Thus, the consequent high relief is the most important controlling factor on the channel orientation, strongly limiting the influence of faults and fracture systems. As a result, (i) the pattern of the drainage network is dendritic and (ii) the main rivers flow transversally to the Massif.

Finally, relicts of a longitudinal paleo-drainage system indicate that the initial SE-sector drainage network was characterized by a planar geometry similar to that currently found in the NW sector of the Massif. This suggests a possible temporal evolution, in the building of a mountain chain, from an initial stage when a drainage geometry is highly dominated by selective erosion along geological structures to a later stage when uplift-induced higher relief forces the drainage into a dendritic transverse system.

Acknowledgements

A preliminary revision of this paper by F. Bigot-Cormier and P. Van der Beek greatly improved the manuscript as well as the review of two anonymous referees.
This work was supported by the National Research Project PRIN 2005.

References


