Taxonomy, evolution and spreading of the turrid genus *Spirotropis* (Gastropoda: Turridae)

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Key words: taxonomy, Turridae, *Spirotropis*, new species, evolution, Europe, Neogene.

The species of the European turrid genus *Spirotropis* are reviewed and the possible pathways of the evolution and spreading of the genus during the Neogene are outlined. Nine species are recognised: *S. spinescens* (Bellardi), *S. badensis* sp. nov. (Middle Miocene, Paratethys), *S. karamanensis* sp. nov. (Middle Miocene, Turkey), *S. tortonica* sp. nov. (Late Miocene, Mediterranean Basin), *S. gramensis* sp. nov. (Late Miocene, North Sea Basin), *S. modiolus* (de Cristofori & Jan) (Early Pliocene, Mediterranean Basin), *S. confusa* (Seguenza) (Pliocene to Recent, North Sea Basin to Mediterranean Basin), *S. monterosatoi* (Locard) (Recent, Morocco to Iberian Basin), and *S. azorica* Bouchet & Warén (Recent, Azores). The ancestral form is *Spirotropis* (s.lat.) *spinescens* (Bellardi) from the Miocene of the Vienna Basin. During the Middle Miocene (Langhian) the genus migrated to the Mediterranean Basin where the species *S. karamanensis* and *S. tortonica* evolved. During the Messinian salinity crisis the genus became extinct in the Mediterranean. In the Atlantic domain *S. gramensis* developed during the Late Miocene in the North Sea Basin. This species was transformed to the Late Pliocene to Recent *S. confusa*. During the Early Pliocene *S. modiolus* occurred in the Mediterranean, but probably died out at Mid-Pliocene. *S. confusa* migrated then from the Atlantic to the Mediterranean during the Late Pliocene. The development of the genus is characterised by the change of the mode of larval development from probably planktotrophic to lecithotrophic which seems to be correlated with progressive cooling of the seawater. The direct larval development became the starting point for a speciation process which led to the formation of several different species in various stratigraphical horizons and geographical regions.

Schlüsselwörter: Taxonomie, Turridae, *Spirotropis*, neue Arten, Evolution, Europa, Neogen.

Die Arten der europäischen Turridengattung *Spirotropis* werden behandelt und mögliche Wege der Evolution und Ausbreitung der Gattung während des Neogens werden aufgezeigt. Neun Arten werden anerkannt: *S. spinescens* (Bellardi), *S. badensis* sp. nov. (Mittel-Miozän, Paratethys), *S. karamanensis* sp. nov. (Mittel-Miozän, Türkei), *S. tortonica* sp. nov. (Ober-Miozän, Italien), *S. gramensis* sp. nov. (Ober-Miozän, Nordsee-Becken), *S. modiolus* (de Cristofori & Jan) (Unter-Pliozän, Mittelmeer-Becken), *S. confusa* (Seguenza) (Pliozän bis rezent, Nordsee-Becken bis Mittelmeer), *S. monterosatoi* (Locard) (Rezent, Marokko bis Iberisches Becken) und *S. azorica* Bouchet & Warén (Rezent, Azoren). Die Stammform ist *Spirotropis* (s. lat.) *spinescens* (Bellardi) aus dem unteren Badenium des Wiener Beckens. Während des Mittel-Miozäns (Langhien) wanderte die Gattung in das Mittelmeergebiet ein, wo sich die Arten *S. karamanensis* und *S. tortonica* entwickelten. Die Gattung starb infolge der Salinitätskrise während des Messins im Mittelmeerbecken aus. Im Atlantik entwickelte sich *S. gramensis* im Ober-Miozän des Nordsee-Beckens. Diese Art entwickelte sich zu der pliozän bis rezent vorkommenden *S. confusa* weiter. Während des Unter-Pliozäns tritt *S. modiolus* im Mittelmeergebiet auf, doch scheint diese im Mittel-Pliozän wieder ausgestorben zu sein. Stattdessen wanderte *S. confusa* im oberen Pliozän vom

Atlantik in das Mittelmeer ein. Kennzeichnend für die Entwicklung der Gattung ist der Wechsel von einem wahrscheinlich planktotrophen Larvalentwicklungs-modus zum lecithotrophen, der offenbar mit der fortschreitenden Abkühlung der Wassertemperaturen zusammenhängt. Die direkte Larvalentwicklung gibt dann Anlaß zu einem Speziationsprozeß mit der Ausbildung mehrerer eigenständiger Arten in verschiedenen stratigraphischen Horizonten und geographischen Gebieten.

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Introduction

The turrid genus *Spirotropis* Sars is known in Europe from the Late Miocene and Pliocene-Pleistocene of Italy, from the Middle Miocene of the Paratethys as well as from Late Miocene and Plio-Pleistocene deposits of the North Sea Basin, and last not least it is also known living in the Mediterranean Sea and the eastern Atlantic from Morocco as far north as Norway. For a long time the genus has been considered to be monotypic containing the only species *S. modiolus* (de Cristofori & Jan) which should have that large stratigraphical and geographical distribution.

In 1832 de Cristofori & Jan described the fossil species *Fusus modiolus* from Early Pliocene deposits of Tabiano, province of Parma, northern Italy. Some years later *Pleurotoma carinata* was described by Bivona (1838) from southern Italy. Bivona, however, did not indicate whether his species was a fossil or Recent one. In any case this name had been applied then to the Recent species known from the Mediterranean Sea. The name *modiolus*, however, uniformly has been used for all the fossil occurrences of the genus which became known: so by Bellardi (1847) for the species found in the Late Miocene of Tortona, by Hörnes (1854) for the specimens of the Badenian clay near Vienna, and by von Koenen (1872) for the species of the Late Miocene of northern Germany and Denmark. The name also has been applied to Pliocene material from Belgium and England.

Di Monterosato (1875) was the first to recognise the identity of the Recent and fossil material and to use the name *modiolus* also for the Recent species. For c. 100 years authors have been following that opinion until Warén (1975) examined the Recent Norwegian population and came to the conclusion that it was not identical with the type of *modiolus*. So he named the Recent form *sarsi*, because the older names had proven to be preoccupied, and he restricted the name *modiolus* to the fossil species. A few years later Bouchet & Warén (1980), in their revision of European deep water Turridae, re-examined the species, confirmed the specific diversity of Recent and fossil material, but used the name *monterosatoi* for the Recent species, a name which had been given for strongly carinated forms from the eastern Atlantic and which had been overlooked by Warén in 1975. Besides this they described a second living species from the Azores, *S. azorica*. In 1984 Bernasconi & Robba examined Pliocene material of *S. modiolus* and, contrary to the opinion of Bouchet & Warén, concluded that Recent and fossil material belong to a single species, because they observed much variability in their measurements of protoconch size and growth ratio which seemed to invalidate the observations of Bouchet & Warén regarding the differences between Recent and fossil material. One year later Bernasconi & Robba (1985) published a paper on the Miocene populations of *Spirotropis*. They maintained the name *S. modiola* for the Miocene species of Italy and northern Germany as well as for the Pliocene and Recent populations, but kept separate from it the species from the Badenian of the Vienna Basin for which they used the name *S. spinescens*. In the same year Palazzi (1985) published a short account of the nomenclatorical history of the species names involved and concluded that as far as the difference between Recent and fossil species is not seriously proved the name *S. modiolus* should be used for all populations. As can be seen from this historical account there remained much incertainty as to the status of the various fossil forms and their relationships to the Recent species.

When comparing specimens of *S. modiolus* which I had collected at the type locality Tabiano, with material from the Miocene of the Vienna Basin and northern Germany and having at hand also some Recent material for comparison it became soon apparent to me that there are more than one or two species involved. The results of my revision of fossil *Spirotropis* are presented in this paper.

Material and methods

Material from the following institutions and private collections has been studied:

FW	collection of Friedrich Weinbrecht, Glücksburg, Germany.
IPUM	Istituto di Paleontologia dell'Università di Modena (Doderlein coll.).
JV	collection of Jaap van der Voort, Ostercappeln, Germany.
KG	collection of Karl Gürs, Eschbach, Germany.
MNHNP	Muséum National d'Histoire Naturelle, Paris, France.
MRSN	Museo regionale di Scienze naturale, Torino, Italy (Bellardi-Sacco collection).
NHMW	Naturhistorisches Museum, Wien, Austria.
RGM	Nationaal Natuurhistorisch Museum, formerly Rijksmuseum van Geologie en Mineralogie, Department of Cainozoic Mollusca, Leiden, The Netherlands.
SMF	Senckenberg-Museum, Molluscan Department, Frankfurt am Main, Germany.
SMNH	Swedish Museum of Natural History, Stockholm, Sweden.

For each species the following shell parameters were measured: diameter of initial whorl of protoconch (nucleus), diameter of the protoconch (last whorl), height of shell, number of whorls (including larval shell and body whorl). Statistical parameters were calculated and compared by means of Students t-test. Values of $t > 3$ indicate a significant difference. Abbreviations: H = hight, n = number, wh = whorls, dnuc = diameter of nucleus, dprot = diameter of protoconch, x = mean value. Numbers of specimens in the paragraphs 'material examined' are indicated as SMF/5 (= 5 specimens in coll. SMF).

Systematical part

Family Turridae
Subfamily Clavinae
Spirotropis G.O. Sars, 1878

1878 *Spirotropis* G.O. Sars, p. 242.

Type species (by monotypy) — *Pleurotoma carinata* 'Philippi' (? = Bivona, 1838) non " 'Defrance' Deshayes", 1834 nec Gray, 1834 = *Drillia confusa* Seguenza 1880.

Spirotropis (s. lat.) *spinescens* (Bellardi, 1847)
(Pl. 1, figs. 1-2)

1838 *Pleurotoma spinescens* 'Partsch', von Hauer, p. 534 (nomen nudum).
1847 *Pleurotoma spinescens* 'Partsch', Bellardi, p. 67 (partim).
1847 *Pleurotoma spinescens* 'Partsch', Michelotti, p. 301 (partim).
1854 *Pleurotoma spinescens* — Hörnes, p. 366, pl. 39, fig. 17.
1891 *Pleurotoma* (o. *Drillia) spinescens* — Hoernes & Auinger, p. 323, pl. 41, figs. 4-8.
1966 *Drillia spinescens* — Strausz, p. 426, pl. 19, fig. 8.
1984 *Spirotropis spinescens* — Bernasconi & Robba, p. 211 (partim), pl. 2, figs. 1-2.

Locus typicus — Baden near Vienna, Vienna Basin, Austria.
Stratum typicum — Grey marl, (Early) Badenian, Middle Miocene.
Material examined — Baden (SMF/13, SMF/5, SMF/2, SMF/3); Soos (SMF/3); Pfaffstätten (SMF/4); Lapugy (SMF/2, SMF/5); Kostej (SMF/17, SMF/16, SMF/13, SMF/2).

Description — Shell moderately large, slender spindle-shaped, with c. 8-9 teleoconch whorls. Whorls with a distinct carination just below mid-whorl and usually 8-9 broadly rounded short axial ribs or knobs which extend from the carina to the lower suture. Whole shell with close set and fine spiral striation; at upper suture with a sutural band formed by some more apparent spiral threads. Last whorl with a strong rib-like bulge or swelling opposite to the mouth. Sinus broad and moderately deep. Sculpture somewhat variable, especially the number of axial ribs or nodes may vary from less than 8 to 10-13 on the last whorl. The variability has been illustrated by Hoernes & Auinger. Siphonal channel moderately long, with spiral striation on its back. Transition from protoconch to teleoconch marked by a distinct flexuous growth mark. Protoconch small, conical, consisting of c. 2.25-2.5 whorls.

Measurements — H: 13.5-17.0 mm, x = 15.25 mm (n = 6), H/n wh: 1.35-1.55, x =

Plate 1

Figs. 1-2. *Spirotropis spinescens* (Bellardi, 1847). 1: Rumania, Kostej (Parau lui Philip), coll. O. Boettger, 1896 (SMF 309847a), x 5; 2: do. (SMF 309847b), x 40. Figs. 3-5. *Spirotropis badensis* sp. nov. 3: Vienna Basin, Soos (holotype SMF 309848), x 5/1; 4: do. (paratype SMF 309850a), x 5; 5: Vienna Basin, Baden (paratype SMF 309852a), x 40.

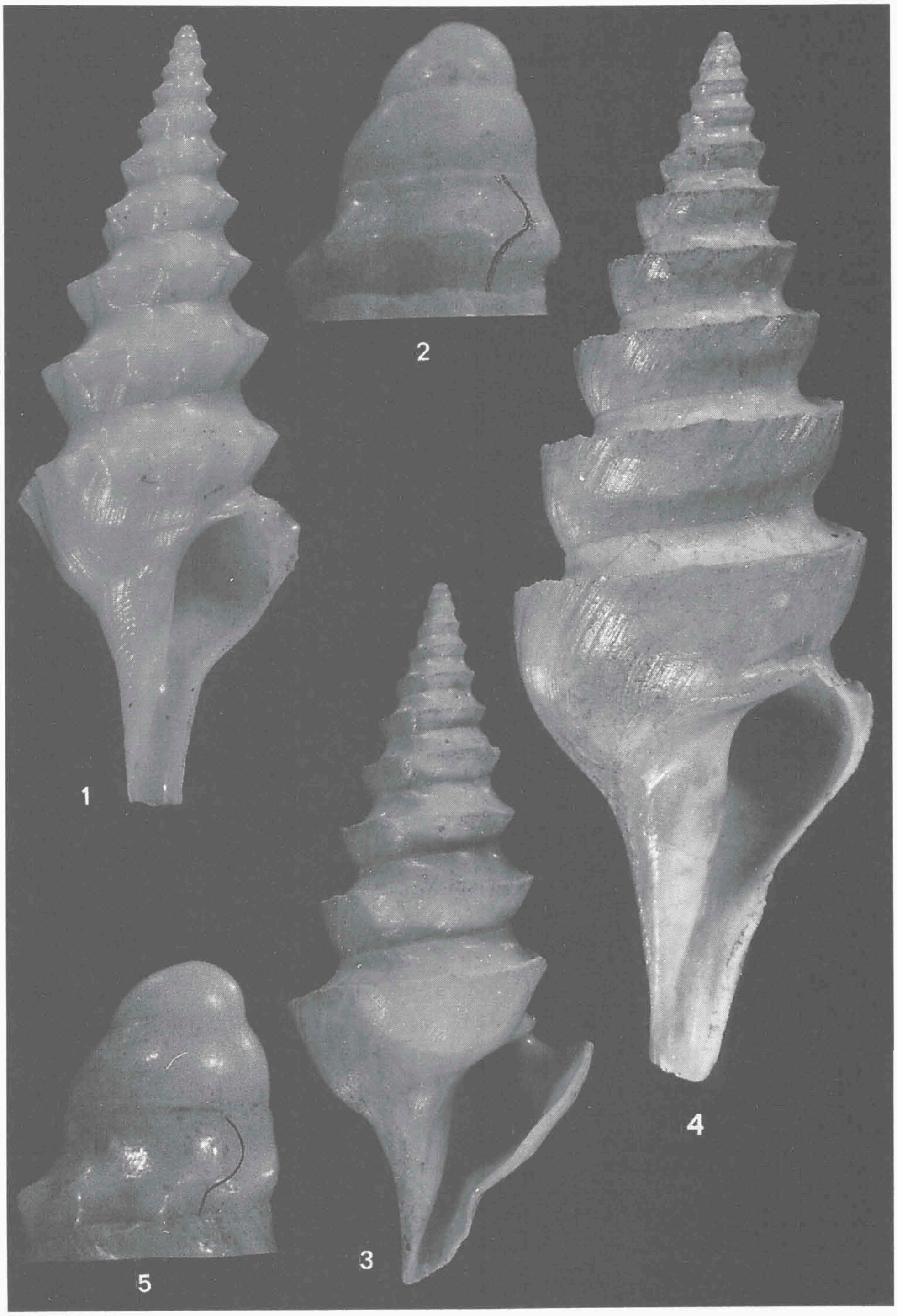

Plate 1

1.474 (n = 6), dnuc: 0.4 - 0.425 mm, x = 0.417 mm (n = 10), dprot: 0.7-0.8 mm, x = 0.747 mm (n = 10).

Remarks — This species obviously is the ancestral form of the typical *Spirotropis* species. There is a close relationship between *S. spinescens* and *S. badensis* sp. nov. (see below), which is demonstrated by the nearly identical protoconch and the vestigial denticulation on early teleoconch whorls in *S. badensis*. In my opinion both species form an evolutionary lineage.

The authorship of this species has been attributed by most authors to Hörnes (1854), who validated most of the manuscript names of Partsch. Bernasconi & Robba (1984) gave Partsch in von Hauer as author. The paper of von Hauer, however, is only a list of fossils with nude names. So the first description of the name is that of Bellardi (1847), resp. Michelotti (1847). The question which author has priority is somewhat difficult to decide. From Sismonda (1847) it is evident, that a separate print of Bellardi's paper (published 1848 in the Memorie della reale Accademia di Scienze di Torino) must have been available in 1847 because Sismonda gave for all of Bellardi's species the reference to his work with pagination of the separate print. As to Michelotti's work Sismonda states (1847, p. viii) that only the plates had been available to him and that he therefore cites only those species of Michelotti which appear on the plates since the whole work had not reached him at the time he gave his synopsis to the printer. From this it is apparent that Bellardi's paper seems to have been published prior to that of Michelotti. The priority of Bellardi can also be inferred from the fact, that Bellardi's monograph is recorded in von Leonhard & Bronn's Neues Jahrbuch für Mineralogie etc., 1848, on p. 57 (early in 1848) whereas Michelotti's work is recorded only on p. 474 (later than June 1848). So it is very probable that Bellardi has priority over Michelotti. The question of priority affects many turrid species named by Bellardi which appear in Michelotti's work and which otherwise would have to be credited to Michelotti. By the validation of the name *spinescens* by Bellardi that name consequently is based on both the material from the Miocene of the Torino hills as well as from the Vienna Basin to which Bellardi refers too. Examination of Bellardi's material from the Torino hills leaves me with some doubts as to its specific identity with the material from the Vienna Basin. Therefore I herewith restrict the name *spinescens* to the material from the Badenian to which the name primarily and usually had been referred. If there are specimens from Vienna in the Bellardi-collection at Torino, a lectotype should be selected from that material. Otherwise a specimen from the Hörnes-collection in Vienna should be designated as neotype in order to stabilise the name.

Because *S. spinescens* is the ancestral species of the typical *Spirotropis* species which are characterised by carinated whorls, it has been included here in that genus. With regard to its sculpture of knobs or axial ribs it could be also classified with *Splendrillia* or a similar genus. This case demonstrates quite well how much one has to consider the possibilities of convergences in shell form and sculpture when classifying fossil turrids without knowledge of their evolutionary relationships.

Spirotropis badensis sp. nov.
(Pl. 1, figs. 3-5)

1837 *Pleurotoma scalaris* 'Partsch', von Hauer, p. 419 (nomen nudum).

1854 *Pleurotoma modiola* — Hörnes, p. 366, pl. 39, fig. 12.
1891 *Pleurotoma* (o. *Drillia*) *modiola* — Hoernes & Auinger, p. 324, pl. 41, figs. 9-10.
1953 *Drillia modiola* — Csepreghy-Meznerics, p. 9, pl. 4, figs. 9-12.
1966 *Spirotropis modiola* — Strausz, p. 427, pl. 19, fig. 7.
1985 *Spirotropis spinescens* — Bernasconi & Robba, p. 211 (partim), pl. 2, figs. 3-5.

Locus typicus — Soos near Baden, Vienna Basin, Austria.
Stratum typicum — Grey marl, (Late) Badenian, Middle Miocene.
Material examined — Soos (holotype SMF 309848, coll. O. Boettger 1901; paratypes SMF 309849/4, coll. O. Boettger 1901; SMF 309850/8, coll. Görges; SMF 309851/5, coll. R. Janssen 1968/1984; other material: SMF/8, coll. O. Boettger, SMF/9, coll. Görges); Baden (paratypes SMF 309852/2, ex F. Rolle; other material: SMF/3, ex F. Rolle, SMF/2, coll. O. Boettger); Vöslau (SMF/1, coll. Kinkelin, SMF/3, coll. Kinkelin, SMF/2, coll. Neuenhaus); Walbersdorf (paratypes SMF 309853/5, coll. Henrich; other material: SMF/2, coll. Henrich, SMF/9, coll. Henrich, SMF/6+2, coll. Neuenhaus, SMF/1, coll. O. Boettger); Möllersdorf (paratypes NHMW/2 = orig. fig. Hoernes & Auinger pl. 41, fig. 9-10).

Description — Shell large for the genus, broadly spindle-shaped, with c. 8-9 teleoconch whorls, which have a very strong and sharp carina at about mid-whorl; edge of carina sharply directed upwards. Whorls deeply concave above the carina. Shell with fine, close-set spiral striation, often with a spiral band below upper suture, growth lines apparent. Carina sometimes irregularly folded, with an *Ancistrosyrinx*-like appearence. First 3-4 teleoconch whorls usually with an obvious blunt denticulation of small nodes and a distinct spiral band below suture. Last whorl with prominent bulge opposite to opening, with a moderately short siphonal channel which bears strong spiral bands on the back. Protoconch with 2.5-2.7 (usually 2.5) whorls, small, conical.

Measurements — Dimensions of holotype: 20 x 8.5 mm, 9.0 teleoconch whorls. H: 17.5-25.5 mm, x = 21.517 mm (n = 12), H/n wh: 1.591-2.125, x = 1.898 (n = 12); dnuc: 0.45-0.525 mm, x = 0.488 mm (n = 15), dprot: 0.75-0.825 mm, x = 0.792 mm (n = 15).

Remarks.— *S. badensis* is clearly distinguished from all other fossil *Spirotropis* by its large size and especially its small conical protoconch of more than two volutions as well as by the denticulation of the initial teleoconch whorls. Its distribution is restricted to the Badenian of the Paratethys.

Bernasconi & Robba (1985) extended the name *S. spinescens* to this species uniting both carinated and strongly knobbed forms to a single taxon. In my opinion the knobbed true *S. spinescens* is clearly distinct from *S. badensis* although they are obviously connected phylogenetically. *S. spinescens* seems to occur in the Early Badenian and is reported also from the Ottnangian (Hörnes, 1876). In the only remaining outcrop of (Late) Badenian clays in Soos near Vienna I have collected only *S. badensis*, but never *S. spinescens* which, however, has been quite frequent in earlier classical outcrops, where apparently also the lower Badenian clay had been exposed. In collections material of both species has not been kept separate according to the stratigraphical level it came from. Also in the very rich fauna from the Early Badenian of Rumania (Kostej, Lapugy) only *S. spinescens* is present. So one can only assume that both species did not occur together at the same level but are confined to the lower and upper level of the Baden clay formation, respectively. Although I could not observe any true intergrading specimens with intermediate characters between *S. badensis* and *S. spinescens* there are some specimens of *S. spinescens* showing a tendency to loosing their axial sculpture on the last whorl. The two species are distinct with regard to the statistical parameters: for dnuc the difference is quite clearly demonstrated by the value of t = 9.396; also different is the growth ratio (H/n wh, t = 7.824, see Fig. 1).

Spirotropis karamanensis sp. nov.
(Pl. 2, figs. 6-8)

Locus typicus — Lale Köy, Akbogazi, Karaman Basin, SE Turkey.

Stratum typicum — Light yellow sandy marl, Middle Miocene, possibly Serravallian (precise age not yet determined, 'Vindobonian' after Erünal-Erentöz, 1956).

Material examined — Lale Köy (holotype SMF 309865, paratypes SMF 309866/1, RGM 229 971/1, coll. JV/4); Akpinar, plateau Pinarlar Yarlesi, 5 km S of Akpinar (paratypes SMF 309867/1, 309868/1, RGM 229 972/2, coll. JV/3, JV/5). All material ex Jaap van der Voort (leg. 1990).

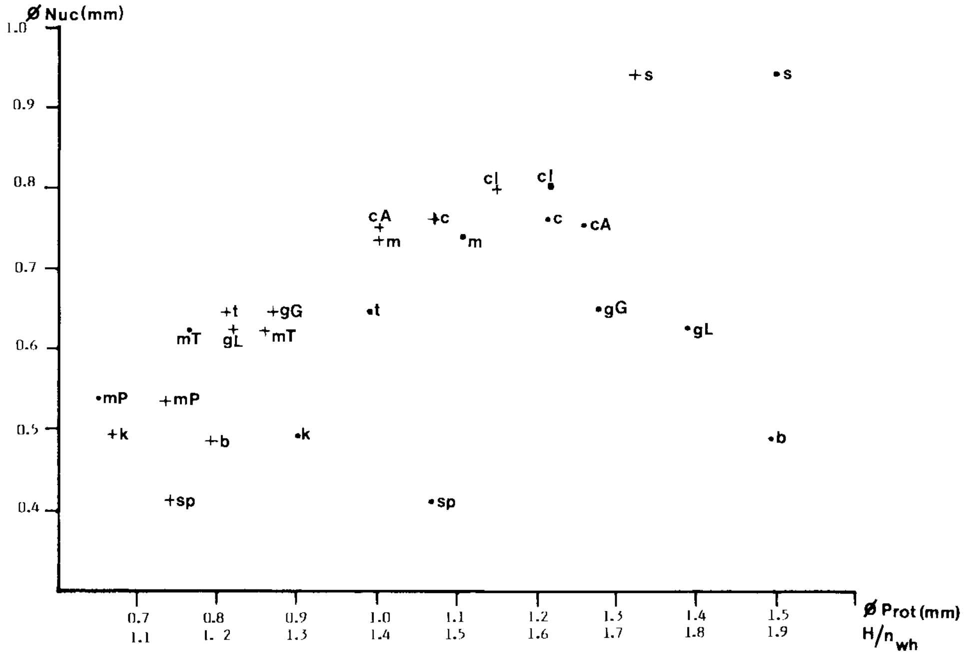

Fig. 1. Shell parameters of *Spirotropis* species. Relation of diameter of initial whorl (nucleus) and last whorl of the protoconch (+) and ratio shell hight/number of whorls (.). The graph demonstrates the variability of the protoconch size in populations of the same species as well as the clear distinction with regard to the parameter H/n wh of species with similar protoconch size; b = *S. badensis*, c = *S. confusa confusa* (Recent), cA = *S. confusa* (Pliocene, Antwerp), cI = *S. confusa* (Plio-Pleistocene, Italy), gG = *S. gramensis* (Gramian), gL = *S. gramensis* (Langenfeldian), k = *S. karamanensis*, m = *S. monterosatoi*, mP = *S. modiolus* (Le Puget-sur-Argens), mT = *S. modiolus* (Tabiano), s = *S. confusa sarsi*, sp = *S. spinescens*, t = *S. tortonica*.

Description — Shell medium-sized, with c. 6-7 teleoconch whorls, smooth and glossy, with sharp carina at mid-whorl or slightly below mid-whorls, carina very sharp and thin. Upper part of whorls sometimes with very weak and hardly visible spiral striation. First teleoconch whorl usually starting with a sharp carina, but some specimens show some very indistinct (3-4) small knobs on the carina. Sinus broad and shallow. Siphonal channel moderately short, with spiral striation on the back. Last whorl with a bulge at about 1/3 whorl in front of the opening. Protoconch very small, conical, of c. 1.5-1.75 whorls, with mammillate nucleus.

Measurements — Dimensions of holotype: 12.2 x 4.9 mm, 7.25 teleoconch whorls. H: 7.8-12.3 mm, x = 10.928 mm (n = 14), H/n wh: 1.114-1.437, x = 1.306 (n = 14); dnuc: 0.475-0.55 mm, x = 0.497 mm (n = 15); dprot: 0.65-0.725 mm, x = 0.678 mm (n = 15).

Remarks — This species is known only from the Miocene of the Karaman Basin. In some characters it holds an intermediate position between *S. badensis* and *S. tortonica* (see below) and probably it represents an intermediate evolutionary stage between these two species. The species is distinguished from *S. badensis* by its small size, a different growth ratio (H/n wh, t = 11.877), the smooth and glossy shell, the smaller protoconch (dprot, t = 14.158), the more or less missing denticulation on the first teleoconch whorl, and by the position of the bulge of the last whorl. From *S. tortonica* it is distinguished by its smooth shell, the smaller dimensions of the protoconch (dnuc, t = 16.757; dprot, t = 12.952) and again by the position of the bulge.

Spirotropis tortonica sp. nov.
(Pl. 2, figs. 9-10)

1842 *Pleurotoma acuta* 'Bellardi', Sismonda, p. 33 (nomen nudum ?; non Perry, 1811) (not seen).
1848 *Pleurotoma modiola* — Bellardi, p. 596, pl. 3, fig. 9.
1877 *Drillia modiola* — Bellardi, p. 129.
1904 *Drillia (Spirotropis) modiola* — Sacco, p. 46, pl. 12, fig. 41.
1937 *Drillia modiola* — Montanaro, p. 153, pl. 7, fig. 17.
1968 *Spirotropis modiola* — Robba, p. 585, pl. 45, fig. 2.
1985 *Spirotropis modiola* — Bernasconi & Robba, p. 210 (partim), pl. 1, figs. 2-4; pl. 2, fig. 6.

Locus typicus — Badlands ('calanci') E of Sta. Agata Fossili, on the right of the road to Bavantore, Province of Piemont, northern Italy.
Stratum typicum — Grey marl, Late Tortonian, Late Miocene.
Material examined — Sta. Agata Fossili (holotype SMF 309854, coll. R. Janssen, 1984; paratypes MRSN Torino BS 0.11.05.062/1-2 orig. fig. Bernasconi & Robba pl. 1, figs. 2-4, pl. 2, fig. 6.; other material: MRSN Torino/many spms.); 'Tortona' (paratypes IPUM 8874/2, coll. Doderlein; additional material: IPUM 8874/18, coll. Doderlein); Montegibbio (IPUM/1).

Description — Shell medium-sized, with c. 7-8 teleoconch whorls, which bear a sharp carina at or slightly below mid-whorl. Shell surface with very fine but distinct spiral striation and a clearly visible spiral band below suture. Initial teleoconch whorl with a few blunt denticulations or knobs on the carina. Last whorl with bulge opposite to opening. Siphonal channel with distinct spiral striation. Protoconch medium-sized, low conical, of 1.5-1.75 whorls.

Measurements — Dimensions of holotype: 13.4 x 5.3 mm, 7.50 teleoconch whorls. H: 10-14.5 mm, x = 12.32 mm (n = 15), H/n wh: 1.167-1.611, x = 1.397 (n = 15), dnuc: 0.6-0.725 mm, x = 0.657 mm (n = 15), dprot: 0.725-0.875 mm, x = 0.817 mm (n = 15).

Remarks — This species is known only from the Tortonian of northern Italy. It is very clearly distinct from both the typical *S. modiolus* as well as the other Miocene species by its usually well developed spiral striation on the whole teleoconch (cf. Bernasconi & Robba, 1985, pl. 1, fig. 4a-b). With regard to protoconch size it is intermediate (but significantly different) between *S. badensis* (dprot, t = 14.158) or *S. karamanensis* (dprot, t = 12.952) and *S. modiolus* (dprot, t = 7.115). The growth ratio, however, does not differ significantly from that of *S. karamanensis* and differs only slightly when compared with *S. modiolus* (see Fig. 1).

Bellardi (1877) recorded *'modiola'* as very rare also from the older Miocene of Torino. Because there is no such material in MRSN in Torino the identity of this record remains questionable. It could be possible that this record refers to *S. karamanensis*. But in any case it indicates that a *Spirotropis* species occurred already earlier than Tortonian in the Mediterranean Basin (see discussion on evolution and spreading of the genus).

Spirotropis gramensis sp. nov.
(Pl. 3, figs. 12-15)

1872 *Pleurotoma modiola* — von Koenen, p. 100.
1956 *Drillia (Spirotropis) modiola* — Rasmussen, p. 82, pl. 7, fig. 6.
1968 *Spirotropis modiola* — Rasmussen, p. 187, pl. 21, figs. 1-4.
1985 *Spirotropis modiola* — Bernasconi & Robba, p. 210 (partim), pl. 1, fig.5.

Locus typicus — Gram, brickyard, South Jutland, Denmark.

Stratum typicum — Dark brown mica clay, Gram Formation, Gramian, Late Miocene.

Material examined — Langenfeldian: Lüneburg (paratype SMF 309856/1), Langenfelde (paratypes SMF 309860/2, ex Philippsen; additional material: SMF/1, coll. O. Boettger; SMF/2, coll. Görges; SMF/3, ex Gottsche), Groß-Pampau (paratypes SMF 309861/1, ex Gürs;, SMF 309862/2, ex Gürs; coll. KG/4; additional material: coll. KG/9); Gramian: Esbjerg (SMF/1), Gram (holotype SMF 309855, ex Weinbrecht; paratypes SMF 309856/1, ex Schnetler; SMF 254420/1, ex Philippsen; SMF 309857/1, coll. Neuenhaus; SMF 309859/2, ex Weinbrecht; RGM 229 962/6, RGM 229 963/3, RGM 229 964/2), Flensburg-Weiche, sandstone (SMF/3, ex Weinbrecht); Syltian: Morsumkliff at Sylt (paratypes SMF 309863/2, ex Kramm; SMF 309864/1, coll. R. Janssen; RGM 220 088/4; additional material: RGM 229 965/1, RGM 229 966/1, RGM 220 088/5 fragm., SMF/5, ex Kramm); Late Miocene: The Netherlands, well Grave-Oss (SMF/2, coll. Görges).

Plate 2

Figs. 6-8. *Spirotropis karamanensis* sp. nov. 6: Turkey, Lale Köy (holotype SMF 309865); x 5, 6a = protoconch, x 40; 7: do. (paratype SMF 309866), x 5; 8: Turkey, Akpinar (paratype SMF 309867), x 5. Figs. 9-10. *Spirotropis tortonica* sp. nov. 9: Italy, Sta. Agata Fossili (holotype SMF 309854), x 5; 10: Italy, 'Tortona' (paratype IPUM 8874), x 5, 10a = protoconch, x 40. Fig. 11. *Spirotropis modiolus* (de Cristofori & Jan, 1832). Italy, Tabiano Bagni, coll. R. Janssen 1984 (SMF 309869), x 5, protoconch x 40.

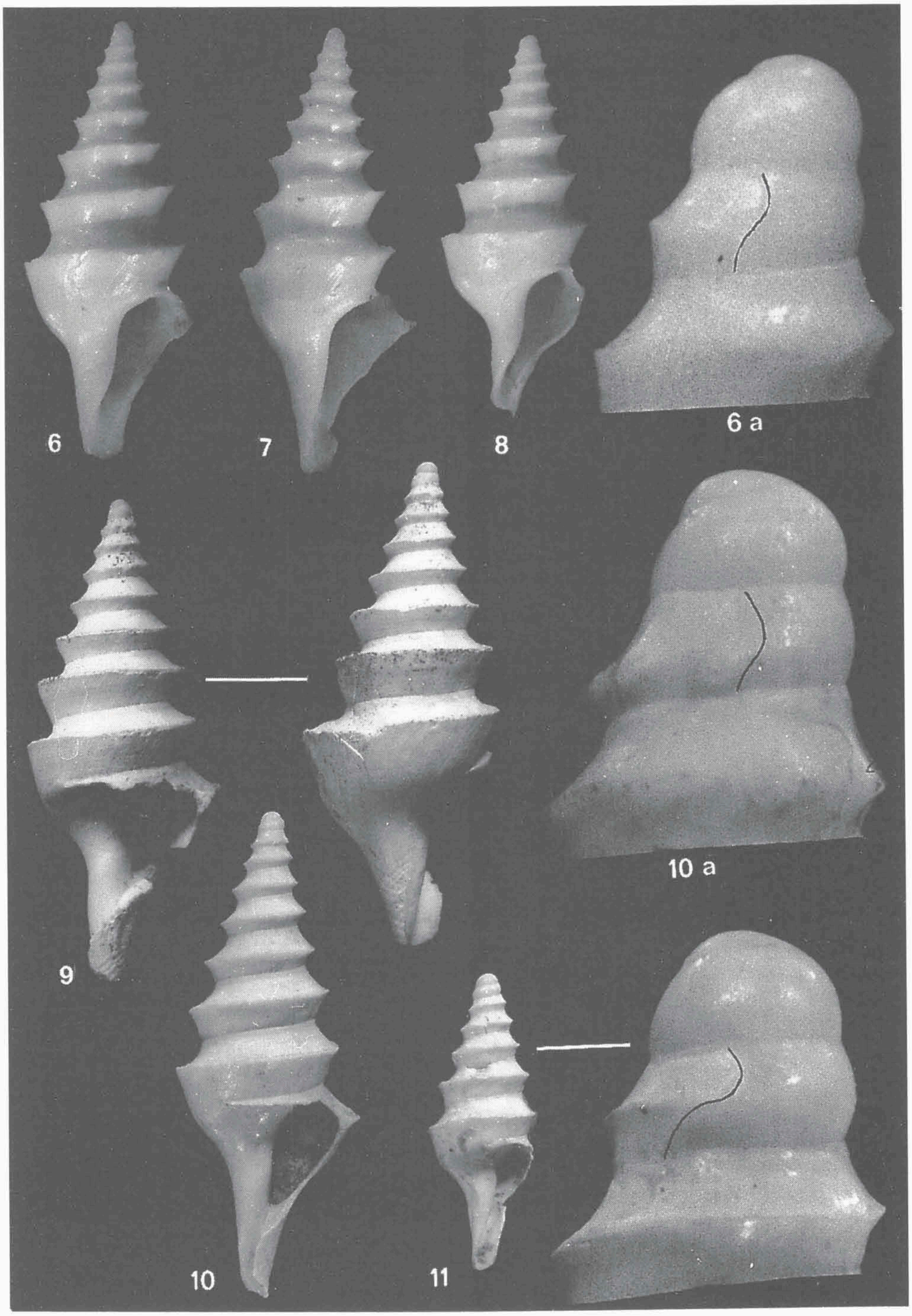

Plate 2

Description — Because populations from the different stratigraphical horizons differ in their characteristics, the various populations are diagnosed here separately:

Langenfeldian: Shell medium-sized, moderately slender, spindle-shaped, with c. 7-8 teleoconch whorls; whorls with a carina at mid-whorl, carina scharp, sometimes with a slightly erected edge; shell usually smooth and somewhat glossy; sometimes there are a few weak spirals visible on the upper part of the whorls. Sinus broad and rather shallow. First teleoconch whorl with sharp carina, without denticulation. Last whorl without bulge, siphonal channel rather short and sculptured with numerous spirals on the back. Protoconch large, mammillate, with 1.5-1.75 whorls.

Gramian: Shell somewhat stout, rather thick-shelled, glossy. Carina far below mid-whorl, often just above the lower suture, broad, bluntly rounded, like a roll. Upper part of whorls with clearly developed spiral striation, sinus broad and shallow. Last whorl and protoconch as described above.

Syltian: Rather slender, spindle-shaped, thick-shelled. Whorls usually with a blunt but quite prominent carina, often sligthly below mid-whorl; sometimes the carina is rather sharp. On the upper part of whorls often with some apparent spiral threads. Sinus broad and shallow. Last whorl and protoconch as described above.

Measurements — Dimensions of holotype: 14.7 x 6.4 mm, 6.75 teleoconch whorls. Langenfeldian: Langenfelde: H: 15-18 mm, x = 16.6 (n = 2); H/n wh: 1.875-2.0, x = 1.937 (n = 2); dnuc: 0.475-0.575 mm, x = 0.525 mm (n = 2), dprot: 0.8 mm, x = 0.8 mm (n = 2). Groß-Pampau: H: 14-16 mm, x = 15 mm (n = 4); H/n wh: 1.555-1.812, x = 1.717 (n = 4), dnuc: 0.6-0.7 mm, x = 0.655 (n = 10), dprot: 0.75-0.9 mm, x = 0.84 mm (n = 10). Gramian: H: 9.6-18.5 mm, x = 13.578 mm (n = 9), H/n wh: 1.371-2.055, x = 1.688 (n = 9); dnuc: 0.6-0.75 mm, x = 0.657 mm (n = 10), dprot: 0.775-0.925 mm, x = 0.857 mm (n = 10). Syltian: H: 15-15.5 mm, x = 15.167 mm (n = 3), H/n wh: 1.667-1.722, x = 1.685 (n = 3); dnuc: 0.625-0.7 mm, x = 0.672 mm (n = 8); dprot: 0.825-0.9 mm, x = 0.862 mm (n = 8).

Remarks — This species is distinguished from *S. modiolus* by its much larger size and a different growth ratio (H/n wh, t = 8.839), from *S. confusa* by its smaller protoconch (dnuc, t = 5.47) and by the distinct spiral striation of the siphonal channel. As indicated in the description the species is somewhat variable in different stratigraphical units: in the Langenfeldian the carina is sharp, whereas in the Gramian and Syltian stages the carina is blunt. Also the diameter of the nucleus is increasing from populations of Langenfeldian to Syltian. The difference in the development of the carina from older populations to younger ones was already observed by Rasmussen (1968, p. 188). Perhaps one could separate the population of the Langenfeldian stage from those of the Gramian and Syltian as a stratigraphical subspecies according to the difference in protoconch size and shape of carina, but with regard to the quite large variability of especially the last character I regard the Late Miocene populations of the North Sea Basin as representing but only one species.

Plate 3

Figs. 12-15. *Spirotropis gramensis* sp. nov. 12: Germany, Groß-Pampau (Langenfeldian) (paratype SMF 309861), x 5, protoconch x 40; 13 Denmark, Gram (Gramian) (holotype SMF 309855); x 5, protoconch x 40; 14: do. (paratype SMF 254420), x 5, protoconch x 40; 15: Germany, Morsumkliff, Sylt (Syltian) (paratype SMF 309863a), x 5.

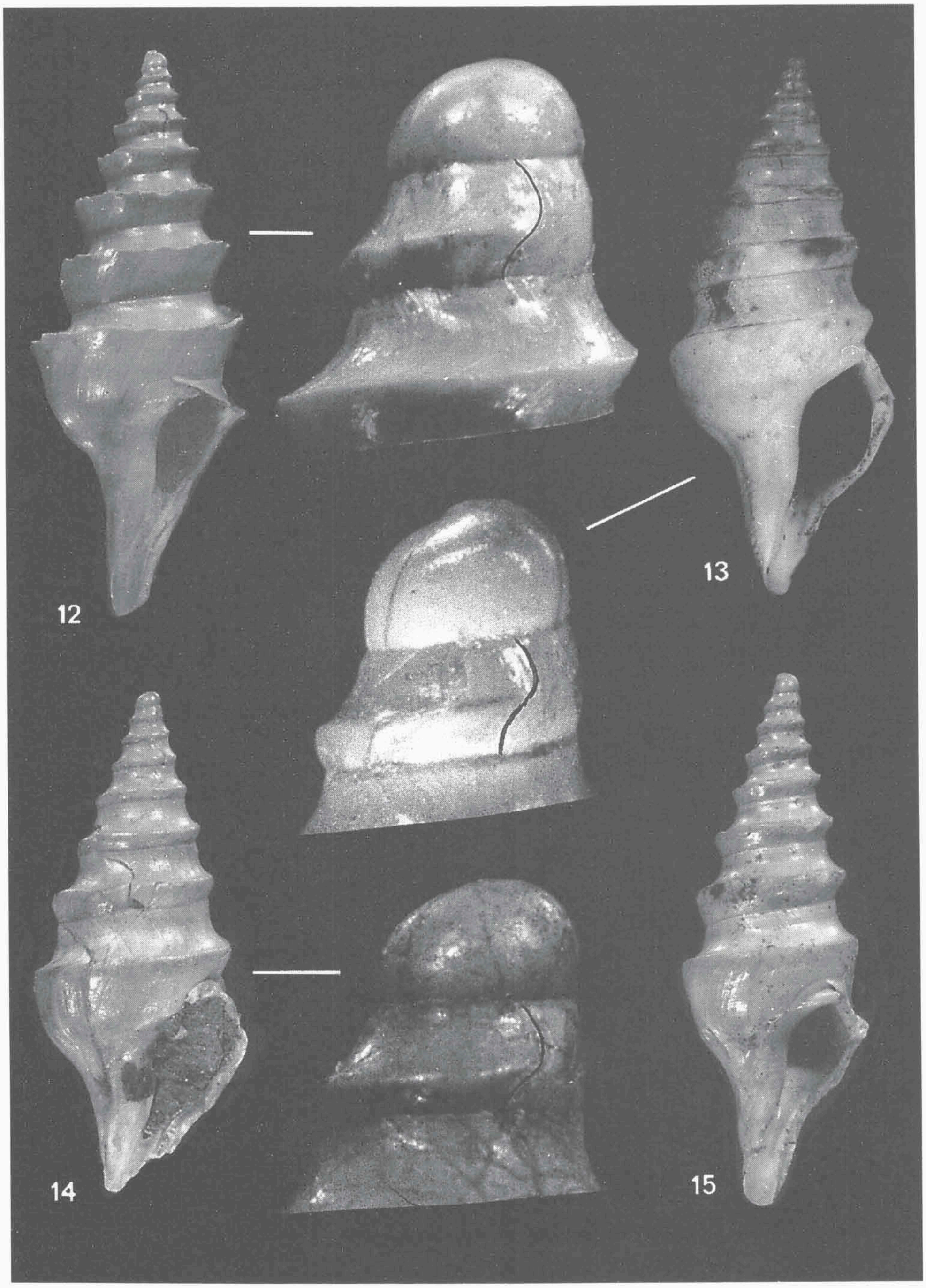

Plate 3

Spirotropis modiolus (de Cristofori & Jan, 1832)
(Pl. 2, fig. 11; Pl. 4, figs. 16-18)

1832 *Fusus modiolus* de Cristofori & Jan, p. 10.
1967 *Spirotropis modiola* — Pelosio, p. 159, pl. 45, fig. 12.
1971 *Fusus modiolus* — Pinna, p. 431, pl. 76, fig. 10 (lectotype).
1978 *Fusus modiolus* — Pinna & Spezia, p. 140, pl. 27, fig. 3 (lectotype).
1984 *Spirotropis modiola* — Bernasconi & Robba, p. 265 (partim), pl. 1, figs. 1-4.
1985 *Spirotropis modiola* — Bernasconi & Robba, p. 210 (partim), pl. 1, fig. 1.
1992 *Spirotropis modiolus* — Cavallo & Repetto, p. 134, fig. 360.

Locus typicus — Tabiano, Province of Parma, northern Italy.
Stratum typicum — Grey clay, Zanclian, Early Pliocene.
Material examined — Italy: Tabiano Bagni (SMF/2, ex della Bella, SMF/9, coll. R. Janssen), Lugagnano (SMF/1, coll. R. Janssen); France: Le Puget-sur-Argens (SMF/c. 100, ex von Hacht; RGM 229 967/20, ex von Hacht).

Description — Shell small, rather slender, with c. 5-6 teleoconch whorls, very smooth and glossy, whorls always with a sharp carina at mid-whorl; carina not cutting, its edge not bent upwards. Last whorl without a bulge, rarely with a very weak swelling at about 1/2 or 1/4 whorl in front of the opening, siphonal channel short, slender, smooth, without spiral striation on the back. Protoconch large, mammillate, of c. 1.5-1.75 whorls.

Measurements — Tabiano: H: 6.4-9.5 mm, x = 7.812 mm (n = 8), H/n wh: 0.966-1.357, x = 1.172 (n = 8), dnuc: 0.6-0.675 mm, x = 0.63 mm (n = 8), dprot: 0.8-0.9 mm, x = 0.859 mm (n = 8); Le Puget: H: 6.1-8.8 mm, x = 7.467 mm (n = 15), H/n wh: 0.871-1.157, x = 1.057 (n = 15), dnuc 0.525-0.575 mm, x = 0.543 mm (n = 15); dprot: 0.675-0.775 mm, x = 0.742 mm (n = 15).

Remarks — This species is confined to the Early Pliocene marls deposited in somewhat deeper water (as can be concluded from the accompagnying fauna, especially at Tabiano). Its constantly small size, smooth and glossy shell and the siphonal channel being devoid of spiral striation distinguish this species from all the Miocene species very distinctly. From *S. monterosatoi* it can be distinguished easily by its small size, the dimensions of the protoconch and the different growth ratio (Tabiano: dnuc, t = 9.049; H/n wh, t = 5.56), compared with *S. confusa* the values are t = 7.756 (dnuc) resp. 7.741 (H/n wh) (see also Fig. 1).

The epithethon specificum '*modiolus*' is a noun used as an apposition. Bernasconi & Robba (1984, 1985) regard the specimen at Milano as the holotype. This is not correct because it is just the only specimen left but it may be possible that somewhere there exist other specimens from the same source (possibly in NHMW). Bernasconi & Robba (1985) united the Miocene populations here distinguished as *S. tortonica* and *S. gramensis*, as well as the Recent '*monterosatoi*' with *S. modiolus* mainly on the basis of the similar apical features and a 'basically similar' growth ratio. But as demonstrated herein measurements taken from much more specimens as well as consideration of qualitative teleoconch features distinctly demonstrate that all these species are clearly separable (Fig. 1).

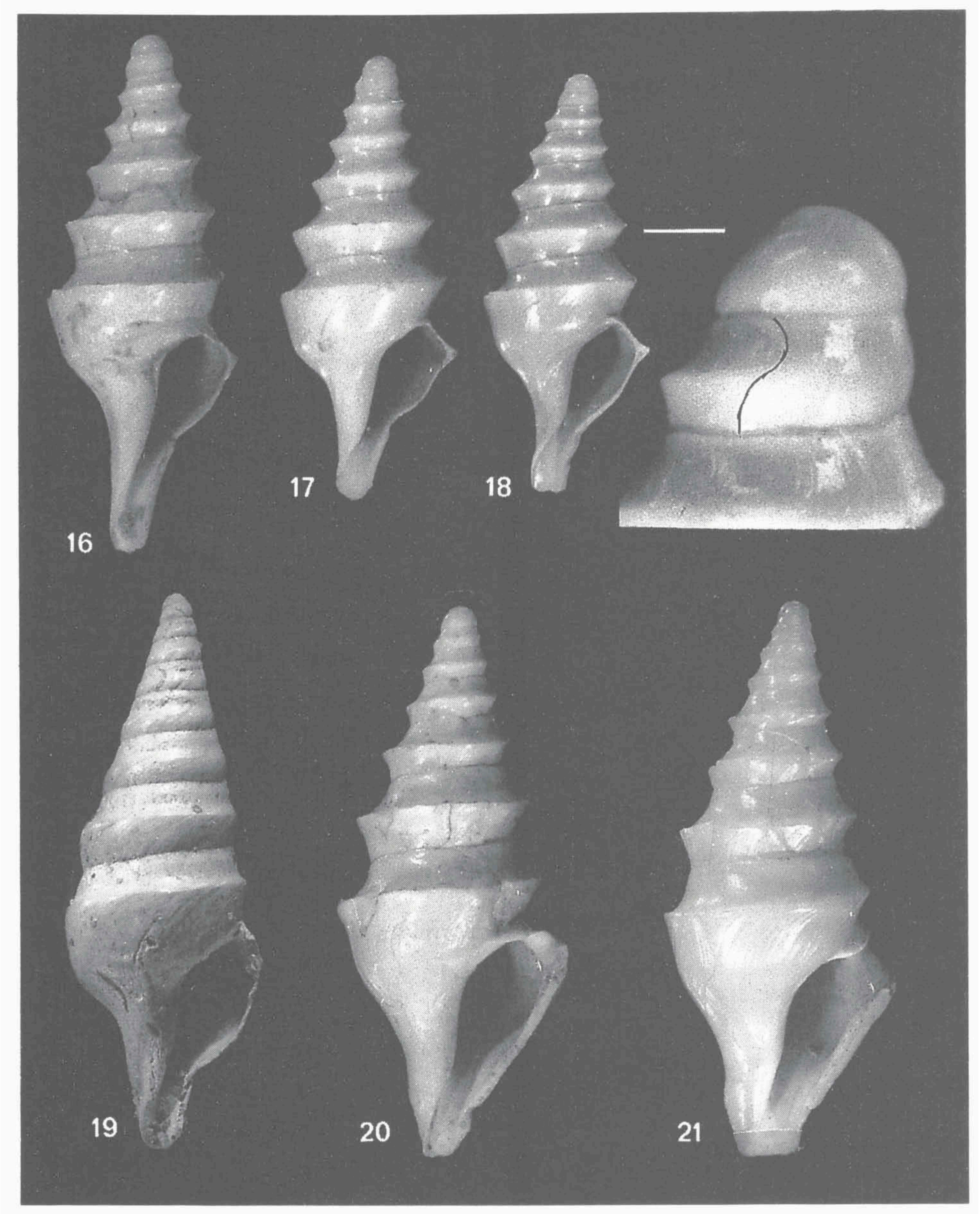

Plate 4

Figs. 16-18. *Spirotropis modiolus* (de Cristofori & Jan, 1832). 16: Italy, Tabiano Bagni (SMF 309869; compare pl. 2, fig. 11), x 8; 17: France, Le Puget-sur-Argens, ex von Hacht (SMF 309870a), x 8; 18: do. (SMF 309870b), x 8, protoconch x 40. Figs. 19-21. *Spirotropis confusa confusa* (Seguenza, 1880). 19: Belgium, Antwerpen (Early Pliocene) (RGM 229 968), x 5; 20: Italy, Crotone (Early Pleistocene) (SMF 309871), x 5; 21: Mediterranean, off Sicily, Poseidon-sta. 172-4, 482-499 m (SMF 309872a), x 5.

Spirotropis confusa confusa (Seguenza, 1880)
(Pl. 4, figs. 19-21; Pl. 5, fig. 22)

?1838 *Pleurotoma carinata* A. Bivona, p. 12 (non Gray, nec Deshayes 1834) (nomen dubium).
1844 *Pleurotoma carinata* — Philippi, p. 176, pl. 26, fig. 19.
1875 *Pleurotoma modiola* — Monterosato, p. 42.
1880 *Drillia confusa* Seguenza, p. 255, 318, 352.
1897 *Pleurotoma modiolum* — Locard, p. 207.
1915 *Spirotropis modiola* — Harmer, p. 230, pl. 28, figs. 9-12.
1960 *Spirotropis modiola* — Glibert, p. 10, pl. 4, fig. 7.
1980 *Spirotropis monterosatoi* — Bouchet & Warén, p. 16 (partim), figs. 52-53, 55-56.
1984 *Spirotropis modiola* — Bernasconi & Robba, p. 265 (partim).
1985 *Spirotropis modiolus* — Palazzi, p. 4.

Locus typicus — *Pleurotoma carinata*: southern Italy (probably Pliocene or Pleistocene); *Drillia confusa*: southern Italy, Calabria: Gerace, Riace, Gallina; Mediterranean Sea (Late Pliocene to Recent).
Material examined — Early Pliocene: Belgium: Kattendijk sands: Antwerpen, Kaai 271 (RGM 229 968/1, RGM 229 969/1 + 8 fragm.); The Netherlands: Ouwerkerk borehole, 119.5-124.75 m (RGM 229 970/6 fragm.). Late Pliocene: southern Italy, Calabria: Boveto (SMNH/1); Early Pleistocene: southern Italy, Calabria: Crotone (SMF/1), Vito Superiore (SMNH/2). Recent: off NW Portugal (Poseidon sta. 1984-1002, 800-900 m, 20.11.1984, SMF/3), off S Portugal (Meteor sta. 8-8a AT 6, 1430-1370 m, 20.1.1967, SMF/1); off Cadiz (Balgim sta. DR 22, 462-472 m, 31.5.1984, MNHNP/11); Mediterranean Sea: Palermo (coll. O. Boettger ex Monterosato, SMF/1), off S. Sicily (Poseidon-sta. 172-4, St.711 Ku, 482-499 m, 6.5.1990, SMF/3), Alboran Sea (Balgim sta. DW 128, 480 m, 14.6.1984, MNHNP/5).

Description — Shell medium-sized, with c. 6-7 teleoconch whorls, usually smooth and glossy, with a carina which is variable from rather prominent to low and blunt. Last whorl always without a bulge, siphonal channel very short and broad, always without spiral striation on the back. Protoconch rather large, dome-shaped, with 1.5-1.75 whorls.

Measurements — Pliocene: Antwerpen: H: not measured because of incomplete specimens, dnuc: 0.725-0.775 mm, x = 0.755 mm (n = 5), dprot: 1.0-1.025 mm, x = 1.005 mm, (n = 5); Recent: off Portugal: H: 11-14.1 mm, x = 12.26 mm (n = 5), H/n wh: 1.443-1.762, x = 1.653 (n = 5), dnuc: 0.7-0.85 mm, x = 0.772 mm (n = 8), dprot: 1.05-1.125 mm, x = 1.084 mm (n = 8); Mediterranean Sea: H: 11.3-14.5 mm, x = 11.72 mm (n = 9), H/n wh: 1.343-1.812, x = 1.590 (n = 9), dnuc: 0.675-0.85 mm, x = 0.755 mm (n = 5), dprot: 1.0-1.1 mm, x = 1.06 mm (n = 5).

Remarks — This species has a wide geographical distribution as well as a wide depth range. The shell is quite variable, especially regarding the development of the carina. Because of the peculiarities of shell sculpture and protoconch size the population from Norway lies far outside the range of variability of the other populations. Therefore I regard it as a distinct race or subspecies *sarsi* (see below). The Pliocene specimens from Antwerp have a more slender, spindle-shaped shell, with a rather low and rounded carina, especially on the early teleoconch whorls there is no true carina but rather a weak shoulder. This form agrees, however, quite well with specimens from Norway. *S. confusa* is distinguished from the fossil species *S. modiolus* by its much larger size, the very much larger protoconch, the growth ratio and the very stout and short siphonal channel. From Miocene species it is clearly distinct because of its shell parameters, the missing bulge of the last whorl and the siphonal channel being avoid of spiral striation.

According to Warén (1975) and Bouchet & Warén (1980) the species *S. carinata* Bivona is a fossil which is not conspecific with the Recent form, but they did not specify the distinguishing characters. After Seguenza *S. carinata* is identical with *S. modiolus* and characterised by its very prominent and sharp carina. He distinguished *S. confusa* from *S. carinata* by its slender shell form and the less prominent non-acute carina, and he states that this form is also found living. Both species, however, occur at least at two localities together (Gerace and Gallina), apparently in the same stratum. It seems very improbable that Seguenza was comparing his *'carinata'* and *S. confusa* with the true *S. modiolus* which has an even much more slender shell than *confusa*. So it might well be possible that the two nominal taxa represent only the two extremes of variability of the development of the carina.

Pleurotoma carinata Bivona is best regarded a nomen dubium. Seguenza (1873-1875) reports *'carinata'* from several localities of Late Pliocene age in southern Italy and Sicily. Bouchet & Warén (1980) regarded *S. monterosatoi* only as an extreme form of *S. confusa*. With the exception of the development of the carina both species are very similar in shell parameters. Only the protoconch diameter shows a slight, but statistically significant difference (t = 4.714). A striking feature, however, is that the animal of *S. confusa* has eyes whereas *S. monterosatoi* is blind (an observation first made by S. Gofas during BALGIM expedition 1984, pers. comm. A. Warén.). *S. confusa confusa* is distributed mainly from the western European Atlantic to the Mediterranean. Its southern limits are not yet determined because of the mixing up of that species with *S. monterosatoi*.

Spirotropis confusa sarsi Warén, 1975
(Pl. 5, fig. 23)

1859 *Mangelia eburnea* M. Sars, p. 84 (non Bivona, 1838).
1878 *Spirotropis carinata* — G.O. Sars, p. 242, pl. 17, fig. 5.
1975 *Spirotropis sarsi* Warén, p. 49, fig. 1 (nom. nov. pro *Mangelia eburnea* M. Sars, 1859 non *Pleurotoma eburnea* Bivona, 1838 = *Mangelia*, et *Pleurotoma carinata* sensu G.O. Sars non Bivona).
1980 *Spirotropis monterosatoi* — Bouchet & Warén, p. 16 (partim), fig. 52.

Locus typicus — Lofoten, northern Norway.
Material examined — Norway, off Stavanger (Senckenberg sta. Nr 13, 290.9-294.8 m, 6.8.1984, SMF/1, Senckenberg sta. Nr 20, 287.1-290.9 m, 7.8.1984, SMF/1); Bergen area (many samples, SMNH/30).

Description — Shell medium-sized to large, with c. 5-7 teleoconch whorls, usually dull or chalky, not glossy, with a broad and bluntly rounded carina. Shell usually with a distinct but fine spiral striation, mainly on upper part of the whorls, and irregular axial foldings or knobbing at mid-whorl. Siphonal channel very broad and short, without spiral sculpture on the back. Protoconch rather large, with 1.5-1.75 whorls.

Measurements — H: 11-14.5 mm, x = 12.11 mm (n = 8), H/n wh: 1.766-2.1, x = 1.899 (n = 8), dnuc: 0.8-1.05 mm, x = 0.95 mm (n = 11), dprot: 1.25-1.425 mm, x = 1.327 mm (n = 11).

Remarks — The Norwegian population is distinguished from the southern populations of *S. confusa* by all shell features, especially by the very large protoconch, to such an extent that it can be separated as a distinct race or subspecies (differences in statistical parameters being highly significant: dnuc, t = 7.551, dprot, t = 12.846, H/n

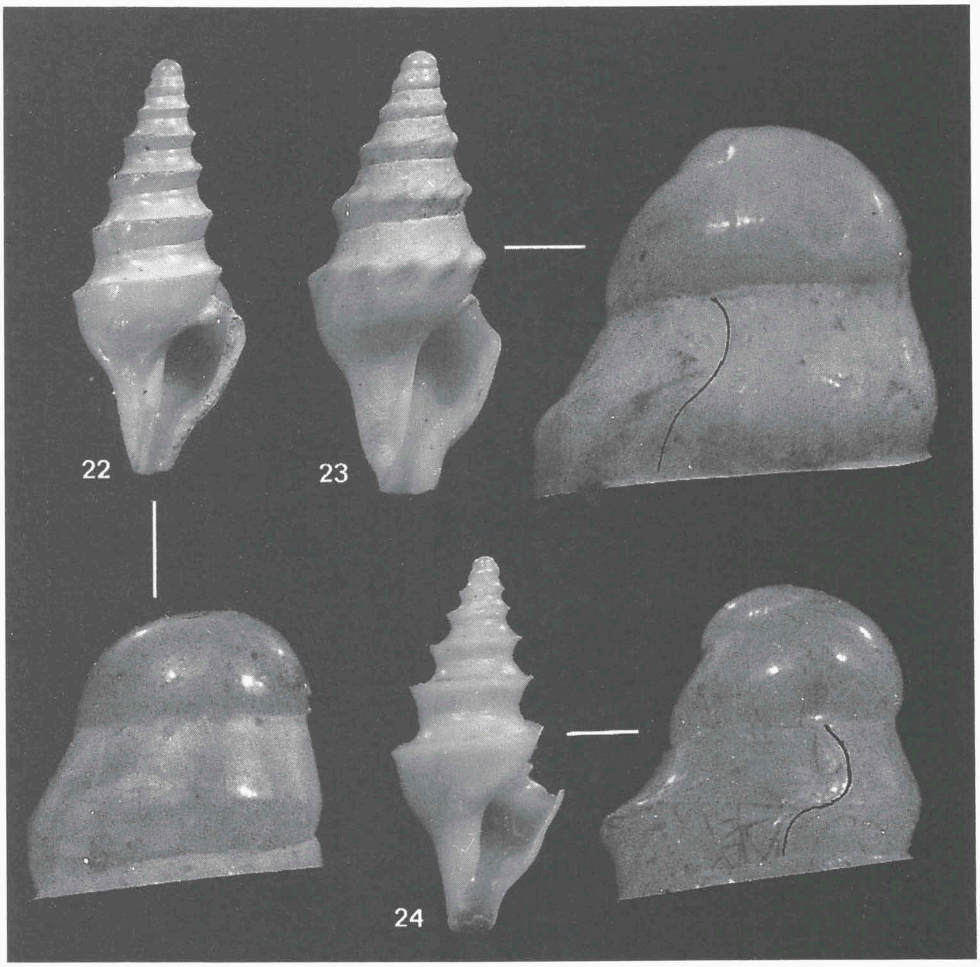

Plate 5

Fig. 22. *Spirotropis confusa confusa* (Seguenza, 1880). Mediterranean, Palermo, coll. O. Boettger ex Monterosato (SMF 309873), x 5, protoconch x 40. Fig. 23. *Spirotropis confusa sarsi* Warén, 1975. Norway, off Stavanger, Senckenberg-sta. Nr 20, 287.1-290.9 m (SMF 309874), x 5, protoconch x 40. Fig. 24. *Spirotropis monterosatoi* (Locard, 1897). Eastern Atlantic, off Morocco, Meteor-sta. 8-19, 1300 m (SMF 309875a), x 5, protoconch x 40.

wh, t = 4.819 when compared with southern populations of *S. confusa*). This seems also justified with regard to the rather restricted distribution of that population which is hardly connected to the southern ones by a few records from North of the Shetland Islands and from the Hebrides (Jeffreys, 1869, p. 221). Apparently this form is undergoing a speciation process leading to become specifically distinct in the course of further evolution. There is no close relationship to the various fossil forms.

Spirotropis monterosatoi (Locard, 1897)
(Pl. 5, fig. 24)

1897 *Pleurotoma monterosatoi* Locard, p. 209, pl. 9, figs. 22-26.
1980 *Spirotropis monterosatoi* — Bouchet & Warén, p. 16 (partim), fig. 57.

Locus typicus — Off NW Morocco, Travailleur 1882 sta. 65, 34°13N, 07°43W, 636 m.
Material examined — Off Cadiz (Balgim sta. DW 20, 450-454 m, 32.5.1984, MNHNP/3); off NW Morocco (Meteor sta. 8-19, AT 9, 1300 m, 26.1.1967, SMF/2; Meteor sta. 36-127, AT 180, 1038-953 m, 12.3.1975, SMF/7; Balgim sta. DR 85, 497 m, 7.6.1984, MNHNP/4).

Description — Shell medium-sized, with c. 5-7 teleoconch whorls, smooth and glossy, often transparent, with a very prominent and sharp carina. Edge of carina usually directed upwards and upper part of the whorls deeply excavated. Usually without apparent spiral striation. Protoconch with 1.5-1.75 whorls.

Measurements — H: 9.5-15.5 mm, x = 11.45 mm (n = 6), H/n wh: 1.357-1.722, x = 1.518 (n = 6), dnuc: 0.675-0.8 mm, x = 0.741 mm (n = 14), dprot: = 0.85-1.075 mm, x = 1.005 mm (n = 13).

Remarks — This species had been united by Bouchet & Warén (1980) with *S. confusa*, but it is separated from that species rather distinctly by its prominent carina and the smaller protoconch diameter (dprot, t = 4.714 when compared with *confusa*). More striking, however, than the only slight conchological difference is the fact that its animal is blind in contrast to *S. confusa* which has eyes (pers. comm. A. Warén). It is difficult to connect *S. monterosatoi* to any of the fossil forms. Perhaps it is somehow related to the Miocene *S. tortonica* but certainly it is not closely related to *S. modiolus*.

The precise distribution of this species is not yet well known because it is often confused with *S. confusa*. It seems to have a more southern centre of distribution (Morocco) and reaches at least to the Iberian Basin where it occurs together with *S. confusa*. Its occurrence in the Mediterranean is questionable.

Spirotropis azorica Bouchet & Warén, 1980

1980 *Spirotropis azorica* Bouchet & Warén, p. 16, figs. 1, 48-51, 59, 192.

Locus typicus — Azores (BIACORES sta 146, 37°40N, 25°36W, 330 m.
Material examined — No material has been examined.

Description — See Bouchet & Warén (1980). Distinct features are the high turreted shell and the rather small protoconch diameter of 0.86 mm.

Remarks — This is another species with an isolated and restricted distribution. Its rather slender shell, small size and small protoconch diameter are somewhat similar to *S. modiolus*, to which it might be related.

Evolution and spreading of *Spirotropis*

(Fig. 2)

A striking feature of the different species of *Spirotropis* is the increase in size of the protoconch from Miocene times until the Recent. Whereas the oldest known species, *S. spinescens* and *S. badensis*, have an apparently short-lived planktotrophic larval development as evidenced by their small conical larval shell of c. 2.5 whorls and the ratio dprot/n prot wh of c. 0.3 (see discussion in Jablonski & Lutz, 1980), all other species have a lecithotrophic mode of development. This fact is very important for the understanding of the history of the genus. The loss of planktotrophy became the starting point of a process of speciation leading to at least nine distinct species each of which is confined to a peculiar faunal province or stratigraphical horizon. The tendency to develop local populations is maintained until today where it can be observed in Recent material from the seamounts of the Eastern Atlantic (pers. comm. A. Warén). As to the taxonomical importance of the mode of larval development see also Bouchet (1990).

The oldest known typical species of *Spirotropis* is *S. badensis* from the Late Badenian of Vienna Basin. This species apparently derived from the knobbed and thus atypical *Spirotropis spinescens* of the Early Badenian of the same region. Probably these species form the ancestral group from which all other species of the genus derived.

The different fossil species being more or less only fragments of lineages it is probably somewhat premature to connect them in evolutionary lineages. Nevertheless the following hypothesis may be a first attempt demonstrating quite clearly the gaps in the reconstruction of the evolution of this genus due to lack of information. The history of the genus can be outlined as follows: Presumably through the passage between the Paratethys and the Mediterranean Basin which existed during early Middle Miocene (Langhian), *S. spinescens* or *S. badensis* migrated to the Mediterranean where closely related forms (*S. spinescens* Bellardi partim and *'modiola'* sensu Bellardi) are known from the Miocene of the Torino hills. During this migration planktotrophy got lost and lecithotrophy was achieved. This process probably had been influenced by a decrease of sea temperature during the younger Miocene.

From *S. badensis* or a *badensis*-like ancestor in the Mediterranean first evolved *S. karamanensis* which is somewhat intermediate between *S. badensis* and the younger species *S. tortonica*. At the same time the genus must have been migrating to the Atlantic where in the North Sea Basin it came to another independent development of *Spirotropis* species. Because in suitable Langhian deposits of the Aquitaine Basin (Saubrigues etc.) no *Spirotropis* is known the genus seems to have reached the Atlantic bioprovince not earlier then Serravallian, from which time on it is known in the North Sea Basin. From southern W-Europe there is no fossil record of the genus known, probably because of unsuitable shallow water facies. In the Mediterranean *S. tortonica* is the last species of the lineage before the genus disappeared during the Messinian salinity crisis. In the North Sea Basin, however, with the beginning of the

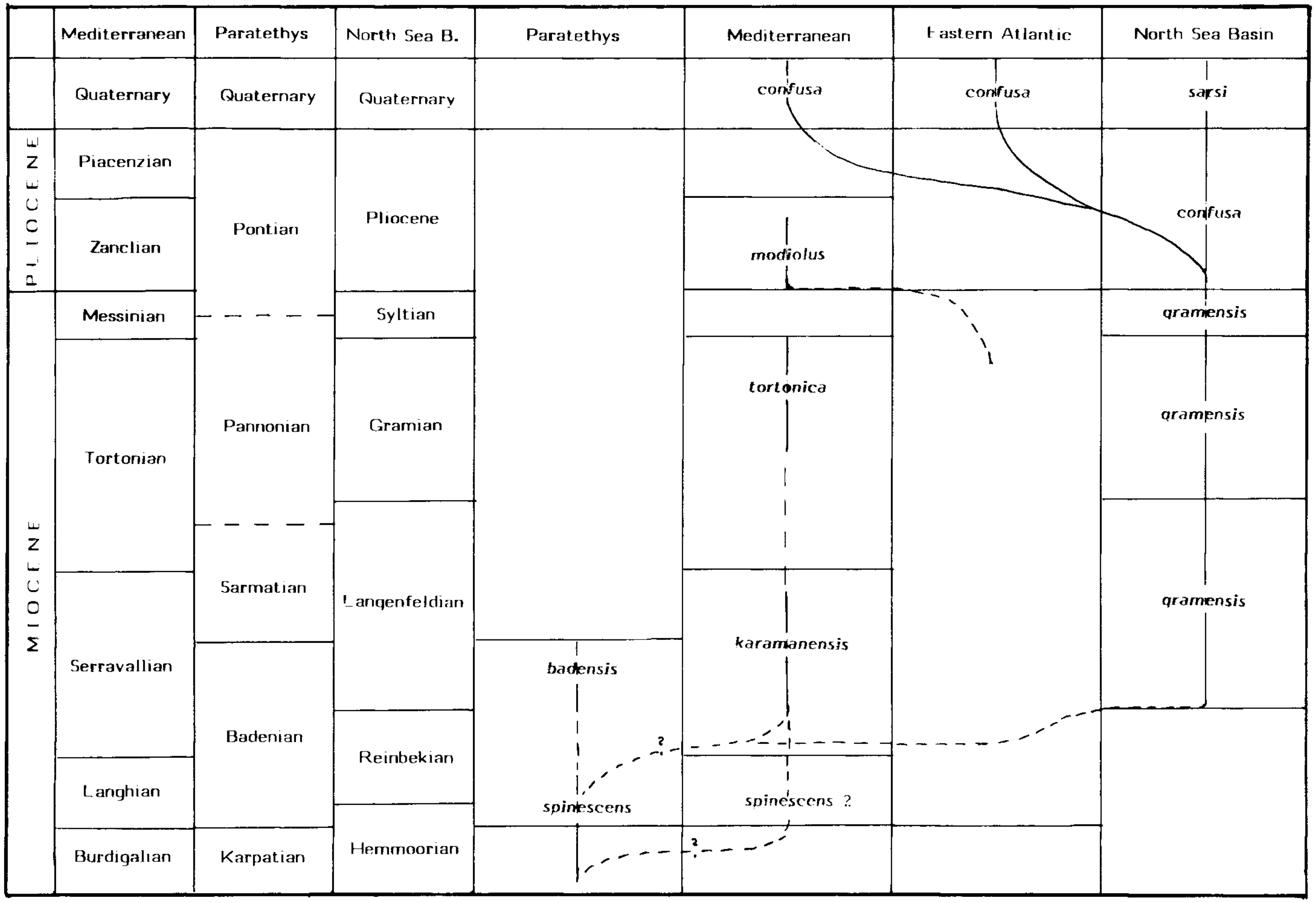

Fig. 2. Possible evolutionary lineages of *Spirotropis* species and their stratigraphical distribution in the European Neogene.

Langenfeldian Stage, that is about early Serravallian in age, *Spirotropis gramensis* suddenly appears without having any ancestor in the Miocene fauna of that region. This species is distinguished from the Mediterranean Miocene species by its much larger protoconch size. During the Late Miocene in this lineage of *Spirotropis* a continuous increase of protoconch (nucleus) size can be observed which changes from c. 0.55 mm in the Early Langenfeldian stage to 0.65 mm in the Late Langenfeldian and further to 0.66 mm in the Gramium and finally to 0.67 in the latest Miocene Syltian Stage. This species of the North Sea Basin is the most probable ancestor of *S. confusa*, a species occurring first in the Early Pliocene of that basin. During the Early Pliocene the genus with the species *S. modiolus* was re-introduced to the Mediterranean from the Atlantic (probably the Lusitanian province). Because there is apparently no record of *Spirotropis* in the Middle and Late Pliocene of northern Italy and only some doubtful citations (because of uncertainty of the species identification) for that time interval in southern Italy (Seguenza, 1880) it is possible that *S. modiolus* became extinct at Mid-Pliocene times - together with many other molluscan species which have disappeared at that time (see Marasti & Raffi, 1980; Raffi & Marasti, 1982). Since there is also a morphological gap between *S. modiolus* and *S. confusa*, it is probable that they are not closely related, and that *S. confusa* migrated during the Late Pliocene from the North Sea Basin into the Mediterranean Sea where it still forms part of the living fauna.

Since the main difference between *S. confusa* and *S. monterosatoi* is an anatomical one (presence and absence of eyes, respectively) it is not possible to trace *S. monterosatoi* in the fossil record with certainty (and it is also possible that fossil specimens of that species are not recognised among *S. confusa* if not showing the very prominent carina). Recent species like *S. monterosatoi* and *S. azorica* presently can not be linked to any of the presumed lineages. They may be derivates of other lineages which may have developed in the Eastern Atlantic during the Late Miocene and Pliocene. Unfortunately there are no fossil records of the genus in the Mio-Pliocene and Quaternary deposits of West Africa and the Lusitanian region.

In conclusion the evolution of the genus *Spirotropis* seems to have taken place in at least two more or less independent evolutionary lineages with different centers of distribution, viz. one in the Paratethys/Mediterranean Basin (mainly Miocene, with *S. badensis* (?) - *S. karamanensis* - *S. tortonica*) and another one in the Atlantic (North Sea Basin) with *S. gramensis* - *S. confusa* from the Late Miocene until the Recent. Both lineages are characterised by the continuous increase of the protoconch size. This striking feature obviously is connected with the decrease of sea water temperature since the Middle Miocene.

From the history of the genus as outlined here it follows that *Spirotropis* is an essentially European genus. Various species from other regions, especially from the Pacific coast of North America which have been assigned to that genus (cf. Grant & Gale, 1931: 548) do not belong here but are classified now with various other genera. Bouchet & Warén (1980) considered *Drillia centimata* Dall, 1889 to belong in the genus *Spirotropis*, but in my opinion that species is better classified with *Leucosyrinx* Dall which shows the same type of planktotrophic protoconch ornamented with faint spiral threads above the suture, a feature never seen in any *Spirotropis* species.

It is obvious that the history of *Spirotropis* is quite complex but can be understood only after critical examination of the various populations which existed during different times in various regions. The genus *Spirotropis* thus is a good example for the process of speciation induced by the change of type of larval development which itself has been triggered by the change of climatic conditions during the younger Neogene.

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