Uncovering the hidden diversity of Paleogene sponge fauna of the East European Platform through reassessment of the record of isolated spicules

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Despite being reported from various localities and stratigraphic intervals, knowledge of the siliceous sponges from the Cenozoic of Eastern Europe remains surprisingly limited. Studies assessing their diversity are almost exclusively in Russian and rather hard to obtain. The most comprehensive elaboration of the sponge spicules from the Paleogene of the East European Platform was published in 2003 and deals with material from Ukraine, Russia, Belarus, and Lithuania. However, the classification in that paper is purely artificial and extremely difficult to interpret according to modern biological criteria. A reassessment of this material is carried out, with the aim of revising all morphotypes of spicules, and identifying them to the lowest possible taxonomic level. Results suggest that the assemblage is much more diverse than previously thought, including members of 24 demosponge families (class Demospongiae), one homoscleromorph (class Homoscleromorpha), and at least one hexactinellid (class Hexactinellida). Our improved understanding of the diversity of Paleogene sponge fauna of the East European Platform will have implications for the interpretation of the past and future ecological and paleobiogeographic studies.

Key words: Demospongiae, Homoscleromorpha, Hexactinellida, spicules, Ukraine, Russia, Eocene.

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Introduction

Modern sponges are inherent components of marine benthic communities with notable ecological roles (Díaz and Rützler 2001; Bell 2008; de Goeij et al. 2013; Mueller et al. 2014; Łukowiak et al. 2018) and substantial share in terms of their biomass (Conway et al. 2001; Hooper et al. 2002; Pansini and Longo 2003; Samaai 2006; van Soest 2007; van Soest et al. 2012). As can be expected, the same is true for Paleogene and Neogene paleocenoses worldwide (Pisera 1999).

To infer the origins of Recent sponge associations, numerous studies have focused on Cenozoic assemblages which have proved to be of unexpectedly diverse and abundant character. These include, for example, rich sponge faunas from the Eocene of Australia and New Zealand (Hinde and Holmes 1892; Hinde 1910; Kelly and Buckeridge 2005; Buckeridge et al. 2013; Łukowiak 2015, 2016; Łukowiak and Pisera 2016) and the Eocene and Miocene of Europe (Pisera and Busquets 2002; Matteucci and Russo 2005; Pisera et al. 2006; Frisone et al. 2014, 2016).

Loose sponge spicules have been described from the Paleogene and Neogene of the Atlantic Ocean (Ivanik 1983; Palmer 1988) and current reports show spicule-rich deposits from the Paleogene of central Ukraine (e.g., Konenkova et al. 1996; Pisera 2000; Ivanova 2014; Stefanska 2014, 2015; Stefanska and Stefansky 2014). Neogene assemblages include spicules from the lower Miocene of the Vienna Basin (Łukowiak et al. 2014), middle Miocene of Poland (Hurcewicz 1991), Portugal (Pisera et al. 2006), Czech Republic (Pisera and Hladilová 2004), Bosnia and Herzegovina (Ivanik 2002), Croatia (Pezelj et al. 2016), and southern Ukraine (Ivanova and Olshtynska 2004).

The most comprehensive study of disassociated sponge spicules from the Paleogene of the East European Platform is that of Ivanik (2003). The study deals with sponge spicules from numerous outcrops and boreholes situated in Ukraine, Russia (the Volga region, Don River Basin, Kaliningrad region), Belarus, and Lithuania. Nevertheless, the morphotypes of spicules described in that study were assessed only artificially and classified within parataxonomic units that are based purely on geometrical characters of the spicules.

Despite the richness of the sponges studied by Ivanik (2003), the study remains virtually unknown and inaccessible as it was published in a book that is hard to obtain and, except for the summary, written in Russian. Moreover, Ivanik (2003) offers only very general and brief discussion of biological meaning of parataxonomically-described material.

Unfortunately, Ivanik's (2003) biological conclusions are only postulative, not demonstrative, i.e., he refers to numerous sponge taxa that supposedly existed in the study area during the Paleogene but does not illustrate the indicated spicule types, preventing independent evaluation. For example, Ivanik (2003) refers to the presence of "lychniscosans" (order Lychniscosida Schrammen, 1903) or *Thrombus* Sollas, 1886, but does not illustrate spicules that belong to these taxa. As such, the results of the study cannot be used directly to interpret sponge evolution, ecology, or paleobiogeography: while the work is comprehensive and rich, the utility of the publication is limited.

The aim of our study is to reassess Ivanik's (2003) material in the light of currently accepted poriferan systematics by revising all spicule morphotypes and classifying them to the lowest possible taxonomic level. We also compare the spicules in Ivanik (2003) to their modern counterparts, allowing inferences of increased diversity to be made about the Paleogene sponges of the East European Platform. The study is expected to serve as a baseline for future ecological and paleobiogeographic reconstructions of ancient sponge fauna of this region.

Assignment of spicules to taxa

The plates published by Ivanik (2003: pls. 1–13) were reassessed following currently accepted systematics (see Boury-Esnault and Rützler 1997; Morrow and Cárdenas 2015) and rearranged to Figs. 1–10, with respect to their taxonomic affinities. The illustrations were slightly edited to improve their quality. Possible taxonomic affinities are summarized in Table 1. The most characteristic spicules are re-described, and their taxonomic position discussed in some detail, below. Additional spicule illustrations of Ivanik (2003: pls. 14–24) are not reproduced or re-illustrated as they are of poor quality, rendering the determination of spicule difficult. However, some of these are referred to in the text, and a reassessment of these spicules is presented briefly in Table 2.

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez, and Boury-Esnault, 2012

Order Tetractinellida Marshall, 1876

Suborder Astrophorina Sollas, 1887

Family Geodiidae Gray, 1867

Geodiidae indet.

Figs. 1C, E, J, N, 2Z.

Material.—Upper and middle Eocene, south-central Ukraine.

Remarks.—The bean-shaped to round massive microscleres with small projections tightly arranged on the spicule surface are considered to be sterrasters (Ivanik 2003: pl. 14: 1, 2, pl. 15: 1, 2; Fig. 1C, E, J, N). They are found in two geodiid genera, *Geodia* Lamarck, 1815 and *Caminus* Schmidt, 1862 (compare Cárdenas et al. 2011 and van Soest et al. 2014: fig. 9). The spherical microsclere (Fig. 1B) may also belong to one of these genera (but affinity with *Placospongia* Gray, 1867 or even Tethyidae cannot be ruled out as well due to poor preservation). Likewise, the big, slender mesotriaenes with a characteristic shaft protruding from the both sides (Fig. 1K, I, V) are probably of geodiid affinity (compare *Geodia garoupa* in Carvalho et al. 2016 or *G. praelonga* in Sim-Smith and Kelly 2015). The same is true for characteristic tetraxial spicule with a long shaft and reduced two clads (Fig. 1W) that may belong to some *Geodia* (former *Isops*) species. Monaxonic spicules with bulb-shaped ending called exotyles (Fig. 5E) could be assigned to *Geodia* (*Isops*) but their vulcanellid, hadromerid, or raspailiid affinity is also possible (see Cárdenas et al. 2011). The same is true for some anatriaenes (Fig. 1L) and orthodichotriaenes (Ivanik 2003: pl. 22: 3; Fig. 1M, AB) which may belong to Geodiidae, Ancorinidae, or Pachastrellidae.

Amongst the illustrated spicules the plesiaster (Ivanik 2003: pl. 20: 2) most likely belongs to a geodiid sponge as well. However, more accurate taxonomic assignment is not possible due to the lack of characteristic features of this spicule.

Moreover, the short-shafted dichotriaene with flat, long leaf-shaped clads (Fig. 2Z) resembles triaenes of modern *Penares* Gray, 1867, especially those of *P. sclerobesa* Topsent, 1904 (compare Topsent 1904: pl. 10: 13). However, also some astrophorid lithistid demosponges are characterized by similar spicule types.

Genus *Erylus* Gray, 1867

Type species: *Erylus mammillaris* (Schmidt, 1862), Azores Canaries Madeira, Adriatic Sea, Recent.

Erylus sp.

Fig. 1A, G, H.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The flat, ellipsoidal spicules called aspidasters (Fig. 1A, G, H) are characteristic for geodiid *Erylus* Gray,

Table 1. Taxonomic affinity of spicules from the East-European Platform and adjacent regions illustrated by Ivanik (2003).

Taxonomical attribution	Figure (this paper)	Plate, respectively (Ivanik 2003)	Spicule	Stratigraphical position (Ivanik 2003)
Astrophorina	1Q	11: 1	centrotylote ?oxea	upper Eocene
	1S	11: 2	plagiotriaene	middle Eocene
	1P, T, U	11: 5, 6, 3	triaenes	upper Eocene
	1R	11: 4	?triaene	lower Eocene
	1I	11: 7	triaene	middle Eocene
	7AB	13: 26	?amphiaster	middle Eocene
?Astrophorina	2N, O	1: 3, 4	oxeas	upper Eocene
	2S	11: 9	?triaene	middle Eocene
Geodiidae	1X	7: 1	mesotriaene	middle Eocene
	1K	7: 10	mesotriaene	upper Eocene
	1V	12: 1	irregular triaene	upper Eocene
?Geodiidae	2W–Y	8: 8, 9, 7	pinakids	upper Eocene
Geodiidae	1W	7: 2	style	middle Eocene
Geodia or *Caminus* sp.	1C, E, J, N	12: 3, 7, 11, 8	sterrasters	upper Eocene
Geodia sp., *Caminus* sp. or Tethyida	1B	12: 12	spheraster	Upper Cretaceous
Geodiidae, Ancorinidae, or Pachastrellidae	7V	4: 10	orthotriaene	middle Eocene
Geodiidae, Vulcanellidae	1M	5: 13	dichotriaene	upper Eocene
Geodiidae, Ancorinidae, or Pachastrellidae	1AB	6: 1	dichotriaene	upper Eocene
Ancorinidae (O), Geodiidae, Ancorinidae, or Pachastrellidae (L)	1L, O	5: 4, 3	anatriaenes	middle–upper Eocene
Geodiidae or Theneidae	1Y, AA	7: 5, 6	diaenes	middle Eocene
Erylus sp.	1A, G, H	12: 10, 6, 9	aspidasters	upper Eocene
?*Dercitus* sp.	2Q	4: 11	orthotriaene	lower Oligocene
?*Penares* sp.	2Z	8: 2	dichotriaene	middle Eocene
Ancorinidae	2E	4: 6	protriaene	middle Eocene
	7S	4: 17	anatriaene	upper Eocene
	2R, 1Z	7: 8, 7	diaenes	middle Eocene
	2K, U, V	6: 4, 5, 6	anadichotriaenes	upper Eocene
Stelletta sp.	2C	4: 4	protriaene	middle Eocene
	2A	4: 7	protriaene	lower Oligocene
	2B, D	4: 8, 9	protriaenes	lower Eocene, lower Oligocene
	2F, J	4: 14 5: 2	anatriaenes	upper Eocene
	2G	4: 16	protriaene	upper Eocene
	2H	5: 6	anatriaene	middle Eocene
	2I	5: 9	prodichotriaene	upper Eocene
	2L, P	5: 10, 12	prodichotriaenes	Cretaceous, middle Eocene
	2T	6: 2	orthodichotriaene	upper Eocene
?*Stelletta* sp.	2M	5: 1	anatriaene	upper Eocene
Pachastrellida	3S	13: 16	?plesiaster	middle Eocene
	3L	3: 18	tylostyle	upper Eocene
	3T	5: 7	calthrop	middle Eocene
	3E	5: 11	prodichotriaene	upper Eocene
	3G	5: 14	dichotriaene	middle Eocene
	3O	6: 9	mesotriaene	middle Eocene
	3D, I–K, P	6: 8, 7, 12, 10, 13	mesotriaenes	lower Eocene
	3U	12: 18	oxyaster	upper Eocene
?Pachastrellidae	3A	4: 15	anatriaene	lower Oligocene
	3F	5: 8	calthrop	lower Eocene
	3C	5: 5	anatriaene	middle Eocene
	3B	6: 3	orthodichotriaene	upper Eocene
Triptolemma sp.	3M, N	7: 17; 11: 12	mesodichotriaenes	upper, lower Eocene

Taxonomical attribution	Figure (this paper)	Plate, respectively (Ivanik 2003)	Spicule	Stratigraphical position (Ivanik 2003)
Pachastrellidae or Calthropellidae	3H	5: 15	dichotriaene	middle Eocene
	3Q, R	9: 12, 14	triods	middle Eocene
Theneidae	4A	4: 5	protriaene	middle Eocene
Alectona sp.	4P, R, T	1: 14, 16, 18	acanthoxeas	upper Eocene
	4O	2: 3	acanthoxea	middle Eocene
	4I–K	9: 9, 10, 8	acanthotriods	middle–upper Eocene
Theonellidae	9E, R	7: 15; 8: 13	phyllotriaenes	middle Eocene
	9H	7: 18	phyllotriaene	upper Eocene
	9A, C	8: 1, 3	phyllotriaenes	Upper Cretaceous, middle Eocene
	9X, Z	8: 17, 11	tetracrepid desmas	lower Eocene, middle Eocene
	9L, O, P	9: 4, 3, 6	phyllotriaenes with ornamented cladome	Upper Cretaceous, middle–upper Eocene
Theonellidae (?*Discodermia* sp.)	9D, F, G	8: 4, 5, 6	discotriaenes	middle–upper Eocene
Pleromidae	9S	8: 18	megaclone	upper Eocene
	9T, U, V, Y	8: 15, 16; 7: 16; 8: 12	megaclones	Upper Cretaceous
	9W	8: 14	?megaclone	Paleocene
	9J, K, N, Q	9: 1, 2, 7; 11: 15	megaclones	Upper Cretaceous, lower Eocene
Samus anonymus	4E, G, H	13: 27; 11: 14; 7: 11	amphitriaenes	upper Eocene
?*Samus anonymus*	4F	7: 12	broken ?amphitriaene	upper Eocene
Tetillidae	4D	1: 11	centrotylote oxea	middle Eocene
?Tetillidae	4B, C	4: 12, 13	anatriaene	upper Eocene
Agelas sp.	4L, M	2: 1, 2	verticillate oxeas	upper Eocene
	4N	3: 14	verticillate style	upper Eocene
Tethyida	5Z	12: 17	oxyaster	middle Eocene
	5AE, AG	12: 19, 20	oxyasters	upper Eocene
	5AF	12: 22	oxyaster	upper Eocene
?Tethyida	5AH, AI	12: 13, 14	spherasters	middle Eocene
	5Y	12: 15	oxyspheraster	middle Eocene
?Axinelliade	5O, P	13: 4, 3	ophirhabds	middle–upper Eocene
Axinellidae	5Q–T	1: 10, 9, 7, 8	flexuous oxeas	middle–upper Eocene
Plocamione sp.	5F–K	13: 18, 19, 20, 21	acanthostrongyles	middle–upper Eocene
?*Plocamione* sp.	5L, N	3: 7, 12	acanthostyles	upper Eocene
	5E	3: 17	exotyle	upper Eocene
	5M	4: 1	acanthostyle	middle Eocene
Janulum sp.	5B–D	2: 13, 14, 15	strongyles	middle Eocene
?*Janulum* sp.	5A	2: 12	strongyle	upper Eocene
Haplosclerida	5AA–AD	13: 7–10	microstrongyles	middle–upper Eocene
Petrosiidae	5V–X	2: 7, 11, 8	strongyles	middle–upper Eocene
Dotona sp.	5U	2: 18	acanthostrongyle	upper Eocene
Placospongia sp.	1D, F	12: 4, 5	selenasters	middle Eocene
Spirastrellidae	6X	12: 21	spheraster	middle Eocene
Sphaerostylus sp.	6B, C	3: 3a, 3b	tylostyles	middle–upper Eocene
	6A	3: 2	spherostyle	middle Eocene
?*Sphaerostylus* sp.	6D	3: 4	tylostyle	middle–upper Eocene
?*Mycale* or ?*Sphaerotylus sp.*	6G	3: 22	exotyle	upper Eocene
Mycale sp.	6H	4: 2	exotyle	middle Eocene
Histodermella sp.	6Y, Z	2: 20, 21	tylotes	middle Eocene
	6N, O	1: 13, 12	acanthoxeas	middle–upper Eocene
Microcionidae	6E, F, J, M	3: 5, 6, 16, 13	acanthostyles	upper Eocene
Myxilla sp.	6I, K	3: 8, 15	acanthostyles	upper Eocene
	6U, V	13: 14, 15	anisochelaes	upper Eocene
Merlia sp.	6L	13: 25	clavidisc	upper Eocene

Taxonomical attribution	Figure (this paper)	Plate, respectively (Ivanik 2003)	Spicule	Stratigraphical position (Ivanik 2003)
Zyzzya sp.	6P–R	2: 19, 16, 17	acanthostrongyles	upper Eocene
?Crellidae	4S	1: 17	sanidaster	upper Eocene
Poecilosclerida	6W	13: 17	isochela	middle Eocene
?Poecilosclerida	6S, T	13: 1, 2	sigmas	upper Eocene
Demospongiae	7C–E	1: 1; 13: 13; 1: 2	oxeas	middle–upper Eocene
	7G	2: 4	acanthorhabd	upper Eocene
	7L, O, Q	2: 22; 3: 1; 7: 3	styles	upper Eocene
	7K, M, N	3: 11, 9, 10	acanthostyles	upper Eocene
	7W, X	3: 20, 19	tylostyles	middle Eocene
	7Z	3: 21	exotyle	upper Eocene
	7P	3: 23	style	middle Eocene
	7R	7: 9	reduced triaene	middle Eocene
	7AC	12: 16	spheraster	upper Eocene
	7T, U	13: 5,6	unknown	upper, middle Eocene
Demospongiae (?Heteroxyidae)	7F, H	2: 5, 6	acanthoxeas	upper Eocene
?Demospongiae	7A, B	1: 5, 6	oxeas	middle–upper Eocene
	7I, J	2: 9, 10	acanthostrongyles	middle–upper Eocene
	7AA	11: 13	fragment of a ?triaene	upper Eocene
Lithistid demosponge	9M	9: 5	siliceous plate (monaxial)	middle Eocene
	9B	12: 2	?sphaeroclone	lower Eocene
Demospongiae or homoscleromorph	8P	5: 16	calthrop	lower Eocene
	8N	6: 14	dichotriaene	middle Eocene
Placinolopha sp.	8I, J	7: 14, 13	lophocalthrops	upper Eocene
	8H, O	11: 8; 13: 24	broken ?lophodiactine	middle Eocene
	8F, G	13: 22, 23	amphiclads	upper Eocene
?*Placinolopha* sp.	8K	11: 11	?lophocalthrop	lower Eocene
Hexactinellida	8C, 10L	9: 16, 15	hexactines	middle–upper Eocene
	10C–E	10: 3, 2, 4	pinular hexactines	upper Eocene
	10F, I, H	10: 5, 7, 8	pinular hexactines	middle Eocene
	10G	10: 6	smooth hexactine	middle Eocene
?Hexasterophora	10K	10: 13	hexactine	middle Eocene
?Lyssacinosida	8B, 10B	9: 14, 13	pentactines	middle Eocene
	10M	9: 17	stauractine	upper Eocene
?Rossellidae	10A	10: 1	pentactine	middle Eocene
	10J	10: 9	tauactine	upper Eocene
?Pheronematidae	9I	10: 10	anchorate spicule	upper Eocene
?Hexactinellida	8D, E	10: 11, 12	?oxeas	middle–upper Eocene
	8A	11: 10	?fragment of dictyonal skeleton	lower Eocene
incerte sedis	7Y, 8M	7: 4; 4: 3	spicule fragment	upper Eocene
	8L	6: 11	spicule fragment	lower Eocene
	9M	11: 15	siliceous plate	middle Eocene
	8Q	8: 10	fragment of a diatom	middle Eocene

1867 (subfamily Erylinae Sollas, 1888; compare Adams and Hooper 2001: fig. 3I). Also other spicules (Fig. 5E, M) and some of the aspidasters (e.g., Fig. 1H), could belong to some other erylinin sponges e.g., *Pachymatisma monaena* Lendenfeld, 1907 (compare Lendenfeld 1907: pl. 35: 21–46). However, this assignment is highly speculative.

Family Ancorinidae Schmidt, 1870

Ancorinidae indet.

Figs. 1O, Z, 2E, H, K, R, U, V.

Material.—Lower, middle–upper Eocene, south-central Ukraine.

Remarks.—Spicules of ancorinid affinity are anatriaenes (Fig. 2H, K, U, V) and diaenes with wavy clads (Figs. 1Z, 2R). The latter ones resemble spicules of modern *Tribrachium* Weltner, 1882 (compare with van Soest 2017: fig. 51F). Also some of the pro- (Fig. 2E) and anatriaenes (Fig. 1O) could belong to ancorinids, e.g., *Ecionemia* Bowerbank, 1862 (compare van Soest and Beglinger 2009: fig. 7).

There are other spicules that could be assigned to Ancorinidae, e.g., those from the Fig. 2Q (?*Dercitus*) and Fig. 10B (?*Stryphnus*; compare Sollas 1888: pls. 15, 6: 4–6); however, the later one can be also a dermal pentactine of Hexactinellida.

Genus *Stelletta* Schmidt, 1862

Type species: *Stelletta grubii* Schmidt, 1862 (type by subsequent designation), Adriatic Sea, Recent.

Stelletta spp.

Fig. 2A–D, F–J, L, P, T.

Material.—Cretaceous, lower Eocene, upper Eocene, lower Oligocene, south-central Ukraine.

Remarks.—Some of the big protriaenes (Fig. 2A, C), prodichotriaenes (Fig. 2I, L, P), and especially the protriaenes with massive shafts (Fig. 2B, D, G), resemble those of ancorinid *Stelletta* (compare Sim 1996: figs. 1–6). The same is true for incomplete anatriaenes (Fig. 2F, H, J, M) and orthodichotriaene (Fig. 2T) that resembles spicules of *Stelletta* (*Myriastra*) illustrated by Sollas (1888: pls. 12 and 14).

Family Pachastrellidae Carter, 1875

Pachastrellidae indet.

Figs. 3D, G–K, O–T, 7Y, 8L.

Material.—Lower Eocene, middle Eocene, upper Eocene, lower Oligocene, south-central Ukraine.

Remarks.—Pachastrellid affinity is apparent for numerous calthrops (Fig. 3T), mesotriaenes (Figs. 3D, I, K, O, P, 8L), mesodichotriaenes (Fig. 3J), and triods (Fig. 3Q, R) (compare Maldonado 2002; Łukowiak and Pisera 2016). A big plesiaster illustrated on the Fig. 3S may also be attributed to pachastrellids. It displays a great similarity to *Characella pachastrelloides* (Carter, 1876) (compare Lévi and Lévi 1989: fig. 33). The same is true for long club-shaped spicule (Fig. 7Y) whose morphology resembles that of the modern pachastrellid *Ancorella paulini* Lendenfeld, 1907 (compare with Lendenfeld 1907: pl. 12: 9). The pachastrellid affinity of some other spicules cannot be ruled out (e.g., Figs. 3A–C, F–H). However, these spicules might also belong to geodiids, calthropellids, ancorinids, or even tetillids.

Genus Triptolemma Laubenfels, 1955

Type species: *Triptolemma cladosum* (Sollas, 1888) (by original designation), Banda Sea, Recent.

Triptolemma sp.

Fig. 3M, N.

Material.—Lower and upper Eocene, south-central Ukraine.

Remarks.—The mesodichotriaenes with variously divided clads (Fig. 3M, N) are identical with spicules of pachastrellid genus *Triptolemma*. They show great resemblance especially to mesodichotriaenes of *T. cladosum* (Sollas, 1888) (compare Sollas 1888: pl. 35: 23).

Table 2. Taxonomic affinity of spicules from the East-European Platform and adjacent regions illustrated by Ivanik (2003).

Taxonomical attribution	Plate (Ivanik 2003)	Spicule
Geodiidae	17: 1–3; 18: 1	sterrasters
Geodiidae (?*Erylus* sp.)	15: 2; 16: 1–3	aspidasters
	14: 2	sterraster (aspidaster)
Geodia or *Caminus* sp.	15: 1	sterraster
?*Geodia* or *Caminus* sp.	14: 1	sterraster
?Geodiidae	20: 2	?plesiaster
Pachastrellidae?	19: 5	oxyspheraster
Astrophorid demosponge	22: 2	prodichotriaene
Demosponge (?Geodiidae)	24: 2	pinakid
Alectona sp.	21: 3, 4	acanthotriods
Lithistid demosponge (Corallistidae?)	22: 3	dichotriaene
Lithistid demosponge (?Theonellidae)	22: 4	tetraclone desma
	23: 2	phyllotriaene
Lithistid demosponge (Pleromidae)	22: 5	megaclone
Lithistid demosponge (?Pleromidae)	23: 1	ornamented dichotriaene
Lithistid demosponge	23: 3	ornamented dichotriaene
Tethyida	19: 4	oxyaster
Plocamione sp.	19: 3	acanthostrongyle
Petrosiidae sp.	18: 2–4	strongyles
?*Mycale* or ?*Sphaerotylus* sp.	20: 7	spherotyle
Histodermella sp.	20: 8, 9; 21: 1	acanthoxeas
Zyzzya sp.	18: 5; 19: 1	acanthostrongyles (verticillate)
	21: 2	acanthostrongyle
?Poecilosclerida	20: 3	sigma
Demospongiae	20: 4	oxea
	20: 5	strongyle
	20: 6	style
	19: 2	acanthostyle
Hexactinellida	23: 4; 24: 1	pinular hexactines
incerte sedis	20: 1	spheraster or ascidian spicule
	22: 1	triod

Family Theneidae Carter, 1883

Theneidae indet.

Fig. 4A.

Material.—Middle Eocene, south-central Ukraine.

Remarks.—The long, thin protriaene (Fig. 4A) may be assigned to Theneidae. This type of spicules appear, e.g., in *Thenea megaspina* Lendenfeld, 1907 (Lendenfeld 1907: pl. 21: 20). The same applies for the diaenes (Fig. 1Y, AA) which resemble spicules of *T. megaspina* Lendenfeld, 1907 (compare Lendenfeld 1907: pl. 21: 21). However, geodiid affinity of the latter spicules cannot be ruled out either.

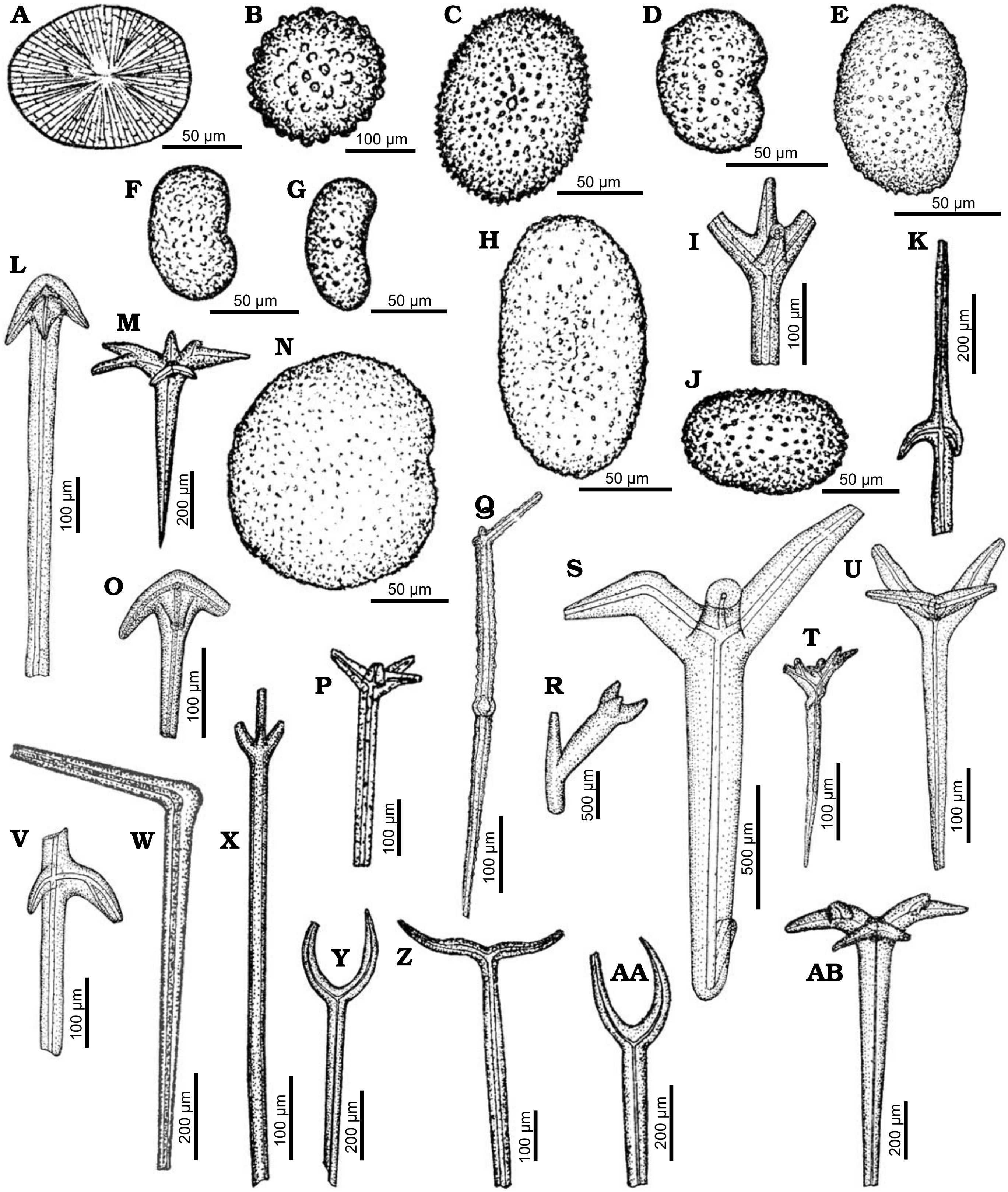

Fig. 1. Spicule morphotypes from south-central Ukraine; Grigorevka borehole, upper Eocene (B), Glâdov Âr, Upper Cretaceous (A, G, J), Pogonovka borehole, upper Eocene (C), Russkie Tiŝki, middle Eocene (D, F, I, O, W, X, Z, AA), Markovka, upper Eocene (E, H, N), Nikol'skoe, upper Eocene (K, L, Q, T, U, V), Pesčanoe, upper Eocene (M, AB), Kantemirovka, upper Eocene (P), Harkov region, middle Eocene (S), Verhnee, lower Eocene (R), and Staroverovka, middle Eocene (Y). **A**, **G**, **H**. Aspidasters. **B**. Spheraster. **C**, **E**, **J**, **N**. Sterrasters. **D**, **F.** Selenasters. **I**. Triaene. **K**, **X**. Mesotriaene. **L**, **O**. Anatriaenes. **M**, **AB**. Dichotriaenes. **Q**. Centrotylote ?oxea. **R**. ?Triaene. **S**. Plagiotriaene. **P**, **T**, **U**. Triaenes. **V**. Irregular triaene. **W**. Style. **Y**–**AA**. Diaenes. After Ivanik (2003); modified.

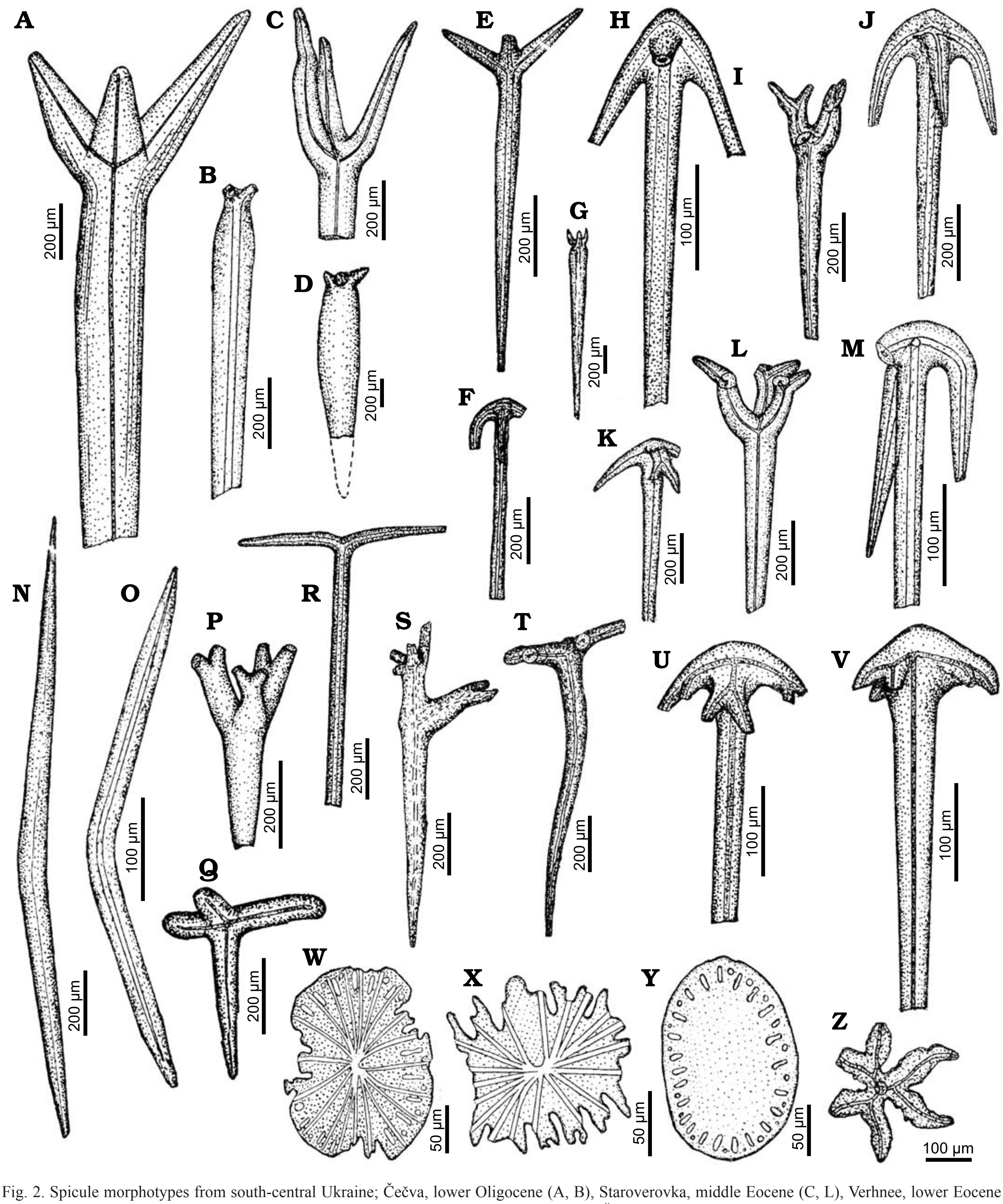

Fig. 2. Spicule morphotypes from south-central Ukraine; Čečva, lower Oligocene (A, B), Staroverovka, middle Eocene (C, L), Verhnee, lower Eocene (D), Russkie Tiŝki, middle Eocene (E, H, R, Z), Nikol'skoe, upper Eocene (F, I, J, K, M, T), Černoleska, upper Eocene (G), Markovka, upper Eocene (N), Melovoe, middle Eocene (O), Glâdov Âr, Cretaceous (P), Markovka, lower Oligocene (Q), Lipcy, middle Eocene (S), Pogonovka, upper Eocene (U), Melovoe, upper Eocene (V), Pesčanoe, upper Eocene (W, Y), and Kiselevka, upper Eocene (X). **A**–**E**, **G**. Protriaenes. **F**, **H**, **J**, **K**, **M**, **U**, **V**. Anatriaenes. **I**, **L**, **P**. Prodichotriaenes. **N**, **O**. Oxeas. **Q**. Orthotriaene. **R**. Diaene. **S**. ?Triaene. **T**. Orthodichotriaene. **W**–**Y**. Pinakids. **Z**. Dichotriaene. After Ivanik (2003); modified.

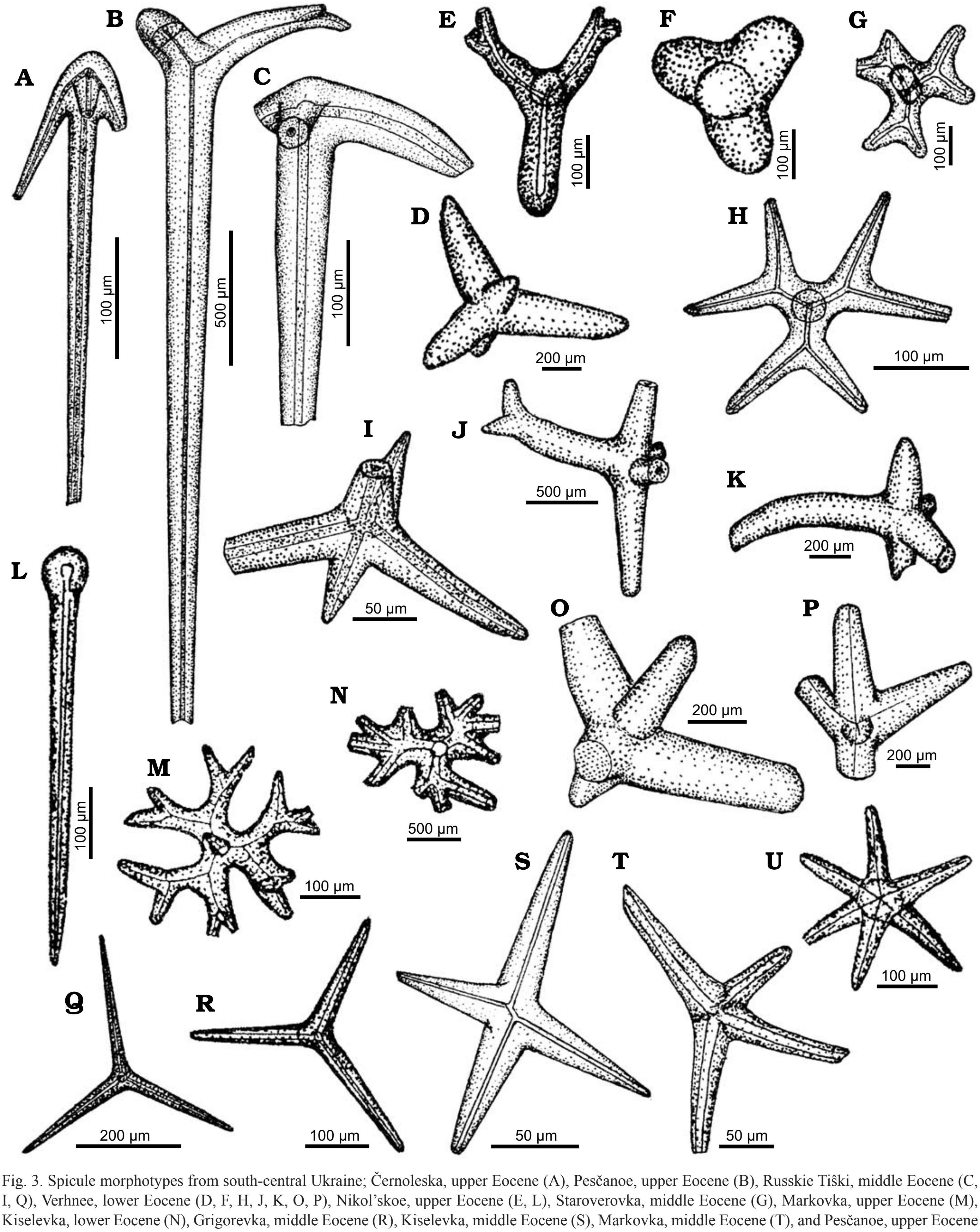

Fig. 3. Spicule morphotypes from south-central Ukraine; Černoleska, upper Eocene (A), Pesčanoe, upper Eocene (B), Russkie Tiŝki, middle Eocene (C, I, Q), Verhnee, lower Eocene (D, F, H, J, K, O, P), Nikol'skoe, upper Eocene (E, L), Staroverovka, middle Eocene (G), Markovka, upper Eocene (M), Kiselevka, lower Eocene (N), Grigorevka, middle Eocene (R), Kiselevka, middle Eocene (S), Markovka, middle Eocene (T), and Pesčanoe, upper Eocene (U). **A**, **C**. Anatriaenes. **B**. Orthodichotriaene. **D**, **I**–**K**, **O**, **P**. Mesotriaenes. **E**. Prodichotriaene. **F**, **T**. Calthrops. **G**, **H**. Dichotriaenes. **L**. Tylostyle. **M**, **N**. Mesodichotriaenes. **Q**, **R**. Triods. **S**. ?Plesiaster. **U**. Oxyaster. After Ivanik (2003); modified.

Family Thoosidae Cockerell, 1925

Genus *Alectona* Carter, 1879

Type species: *Alectona millari* Carter, 1879 (by monotypy), Celtic Sea, Recent.

Alectona spp.

Fig. 4I–K, O, P, R, T.

Material.—Middle–upper Eocene, south-central Ukraine.

Remarks.—The spiny triactines (also called acanthotriods) with long rays covered with spines regularly arranged in whirls (Ivanik 2003: pl. 21: 3, 4; Fig. 4I–K) resemble those of *Alectona triradiata* Lévi and Lévi, 1983 (compare Bavestrello et al. 1998: fig. 2a–c). However, the spicules of modern *Alectona* possess very well developed spines also on the ray tips while those from Ukraine lack the spines on the tips. Although, this difference in spines arrangement may be due to the poor preservation state of the fossil spicules.

In turn, the long, bent oxeas that are rather irregularly covered by minute spines (Fig. 4P) show great resemblance to spicules of modern *Alectona primitiva* Topsent, 1932 (compare Vacelet and Vesseur 1971: fig. 22).

The smaller acanthoxeas (Fig. 4O, R, T) are less bent in the middle of its shaft and regularly covered with minute spines. They are almost identical with the spicules of modern *Alectona millari* Carter, 1879 (compare Carter 1879: pl. 17: 3). The acanthorhabds (Fig. 4S), in turn, might be of alectonid affinity because similar spicules (diactines) have been described by Bavestrello et al. (1998) and assigned to *Alectona* sp. (see Bavestrello et al. 1998: fig. 7). Still, these spicules also resemble sanidasters of *Crellastrina alecto* Topsent, 1898 and spicules of some species of *Halicnemia* Bowerbank, 1864 (Stelligeridae; van Soest 2017: fig. 34).

Family Theonellidae Lendenfeld, 1903

Theonellidae indet.

Fig. 9A, D–H, L, O, P, R, U, X, Z.

Material.—Lower Eocene, middle–upper Eocene, Upper Cretaceous, Paleocene, south-central Ukraine.

Remarks.—The most common lithistid spicules reported by Ivanik (2003) seem to belong to the family Theonellidae. These are mostly ectosomal phyllotriaenes (Fig. 9A, E, H, U), as well as discotriaenes (Fig. 9D, F, G). Such spicules are characteristic for *Discodermia* du Bocage, 1869 (discotriaenes) and *Theonella* Gray, 1868 (phyllotriaenes) and closely related genera. Presence of one or more of these genera is also supported by occurrence of rare fragmentary preserved tetraclone desmas (Fig. 9S, X, Z) that are characteristic for this family.

The ectosomal phyllotriaenes with complex morphology of the cladome (Fig. 9L, O, P) resemble those found in an undescribed theonellid sponge taxon from the Salomon Islands (AP unpublished material).

Family Pleromidae Sollas, 1888

Pleromidae indet.

Fig. 9J, K, N, Q, S–W, Y.

Material.—Lower Eocene, Upper Cretaceous, south-central Ukraine.

Remarks.—Pleromidae are commonly represented by smooth megaclones. Despite that some of the illustrated megaclones (Fig. 9J, K, N, Q, T–W, Y) are Late Cretaceous, the same type of spicules was also found in the Paleogene deposits (e.g., Fig. 9S, see figure caption).

Suborder Spirophorina Bergquist and Hogg, 1969

Family Samidae Sollas, 1888

Genus *Samus* Gray, 1867

Type species: *Samus anonymus* Gray, 1867; by monotypy.

Samus anonymus Gray, 1867

Fig. 4E, G, H.

Material.—Middle–upper Eocene, upper Eocene, south-central Ukraine.

Remarks.—The spicules illustrated on the Fig. 4E and the partially preserved spicules on the Fig. 4G, H are amphitriaenes. These highly diagnostic spicules are almost identical in size (clads about 50 μm long) and shape with spicules of modern spirophorid sponge *Samus anonymus* Gray, 1867 (compare van Soest and Hooper 2002: fig. 1). The broken amphitriaene from the Fig. 4F seems to belong to *Samus* as well.

Family Tetillidae Sollas, 1886

Tetillidae indet.

Fig. 4D.

Material.—Middle and upper Eocene, south-central Ukraine.

Remarks.—The stout centrotylote oxea of about 230 μm of length (Fig. 4D) is of great morphological resemblance, and the same size, as the spicules of tetillids (compare e.g., *Acanthotetilla gorgonosclera*, van Soest 1977: fig. 4e). However, similar spicules can be found in geodiids (van Soest 2017: fig. 55d) and thoosids (e.g., Carballo et al. 2004: fig. 21d). The long thin anatriaenes (Fig. 4B, C) and acanthoxea (Fig. 6N) could belong to tetillids as well. The acanthoxeas of similar morphology are found, e.g., in *Acanthotetilla walteri* Peixinho, Fernandez, Oliveira, Caires, and Hajdu, 2007 (Peixinho et al. 2007: fig. 7c), but their coelosphaerid affinity is more likely.

Order Agelasida Hartman, 1980

Family Agelasidae Verrill, 1907

Genus *Agelas* Duchassaing and Michelotti, 1864

Type species: *Agelas dispar* Duchassaing and Michelotti, 1864 (by subsequent designation; Burton and Rao 1932), Eastern Caribbean, Recent.

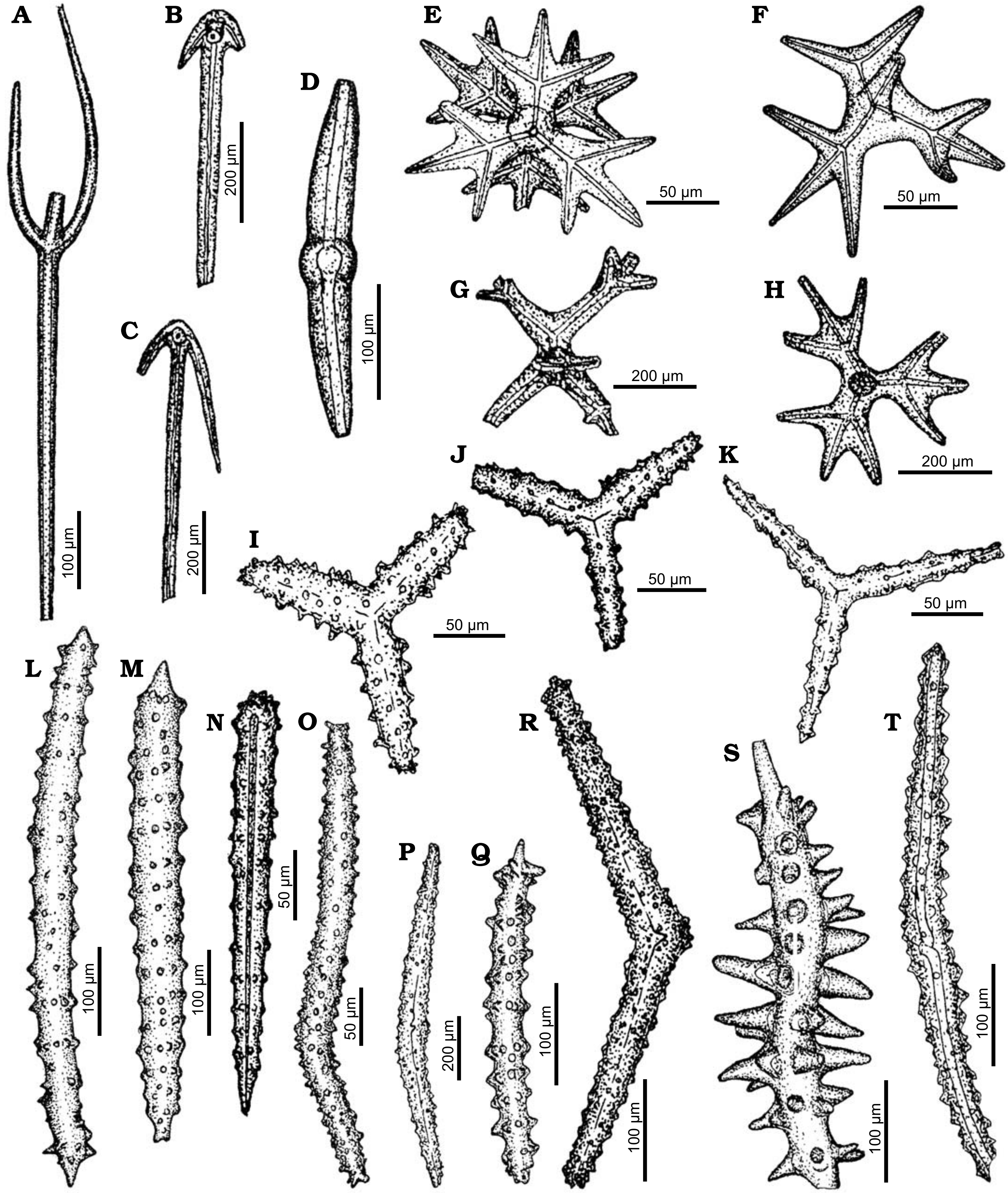

Fig. 4. Spicule morphotypes from south-central Ukraine; Russkie Tiŝki, middle Eocene (A, O), Nikol'skoe, upper Eocene (B, C), Kantemirovka, middle Eocene (D), Melovoe, upper Eocene (E), Staroverovka, middle Eocene (F), Kantemirovka, upper Eocene (G, I), Markovka, upper Eocene (H, N), Pogonovka borehole, upper Eocene (J, L, M), Markovka, middle Eocene (K, P, T), Kiselevka, middle Eocene (Q), Lipcy, middle Eocene (R), and Kiselevka, upper Eocene (S). **A**. Protriaene. **B**, **C**. Anatriaenes. **D**. Centrotylote oxea. **E**–**H**. Amphitriaenes. **I**–**K**. Acanthotriods. **L**, **M**. Verticillate oxeas. **N**. Verticillate style. **O**–**R**, **T**. Acanthoxeas. **S**. Sanidaster. After Ivanik (2003); modified.

Agelas spp.

Fig. 4L–N.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The long verticillate oxeas illustrated on Fig. 4L, M belong to *Agelas*. These spicules are equipped with 18 whorls of short tubercles regularly arranged along the spicule. They are similar with acanthoxeas of modern species of *Agelas*, especially *A. axifera* Hentschel, 1911 and *A. sansibarica* Perino and Pronzato in Manconi et al., 2016. These two species have in their skeletons verticillated oxeas of almost identical morphology (compare Hentschel 1911: fig. 54 and Manconi et al. 2016: fig. 3). The spicules illustrated by Ivanik (2003) seem to exhibit a greater resemblance to spicules of *A. sansibarica* as they are of comparable length and possess a similar number of whorls.

There is also one verticillate style (Fig. 4N) with regular whorls of tubercles that could be assigned to one of the *Agelas* species (compare spicules of *Agelas ceylonica* Dendy, 1905, illustrated by Manconi et al. 2016: fig. 11e).

Order Tethyida Morrow and Cárdenas, 2015

Tethyida indet.

Fig. 5Y, AE, AF, AG.

Material.—Middle Eocene, upper Eocene, Upper Cretaceous, south-central Ukraine.

Remarks.—The oxyaster shown on the Fig. 5AF clearly belongs to Thetyida. This spherical spicule with divided ray tips is about 150 μm in diameter and might belong to some species of *Timea* Gray, 1867 (Timeidae; *Timea diplasterina* Rützler, Piantoni, van Soest, and Díaz, 2014: fig. 125c). However, it could also belong to *Tethya* Lamarck, 1815 (Tethyidae; compare Sarà 2002: fig. 9e). Also, various asters (~60–150 μm in diameter) might belong to *Tethya* (Figs. 1B, 5Y, AE, AG).

Order Axinellida Lévi, 1953

Family Axinellidae Carter, 1875

Axinellidae indet.

Fig. 5Q–T.

Material.—Middle–upper Eocene, south-central Ukraine.

Remarks.—Among the illustrated spicules, the 200–480 μm long flexuous oxeas (Fig. 5Q–T) may show axinellid affinities. However, flexuous oxeas are also characteristic for the heteroscleromorph family Bubaridae (compare Alvarez and van Soest 2002). Still, owing to the general shape and thickness of the discussed spicules, their attribution to Axinellidae is more likely.

Family Raspailiidae Nardo, 1833

Genus *Plocamione* Topsent, 1927

Type species: *Plocamione dirrhopalina* Topsent, 1927 (by monotypy), Azores, Canaries, Madeira (geounit), Recent.

Plocamione spp.

Fig. 5F–K.

Material.—Middle–upper Eocene, south-central Ukraine.

Remarks.—The spicules illustrated on the Fig. 5J, K and in Ivanik (2003: pl. 19: 3) are identical with spicules of the two raspailiid species, *Plocamione carteri* (Ridley and Duncan, 1881) and *P. dirrhopalina* Topsent, 1927. The skeleton of these two species possesses choanosomal acanthostrongyles (compare Hooper 2002: fig. 20d) of comparable size (50 μm in living and 34 and 45 μm in fossil representatives; Ridley and Duncan 1881: pl. 23: 19). The morphologies of the other choanosomal acanthostrongyles, illustrated on the same figure are very similar too (Fig. 5F–I). The style from the Fig. 3Q may belong to some *Plocamione* species as well (compare Hooper 2002: fig. 20a). Nevertheless, its vulcanellid affinity cannot be ruled out either.

The same is true for the long acanthostyle illustrated on the Fig. 5M which resembles the spicules belonging to the recent taxon *Plocamione pachysclera* (Lévi and Lévi, 1983) (compare *Raspailia pachysclera* Lévi and Lévi, 1983: fig. 12.2; Hooper 2002: fig. 20j). They are identical in terms of their morphology and size. Still, similar spicules also appear in erylinid *Pachymatisma monaena* Lendenfeld, 1907 (Lendenfeld 1907: pl. 35: 35).

The spicules illustrated on the Fig. 5E, L, N may belong to *Plocamione* as their morphology and size is comparable with some spicules of this extant genus (compare with Hooper 2002: fig. 20d).

Genus *Janulum* Laubenfels, 1936

Type species: *Janulum spinispiculum* (Carter, 1876) (type by original designation), South European Atlantic Shelf, Recent.

Janulum sp.

Fig. 5B–D.

Material.—Middle Eocene, south-central Ukraine.

Remarks.—The strongyles (Fig. 5B–D) are similar in size (165–250 μm) and morphology to acanthostrongyles of the modern raspailiid genus *Janulum* (compare Kelly et al. 2015: figs. 2, 3). The fossil spicules seem to have some signs of erosion in places where the spines in the modern spicules originate.

Order Haplosclerida Topsent, 1928

Family Petrosiidae van Soest, 1980

Petrosiidae indet.

Fig. 5V–X.

Material.—Middle–upper Eocene, south-central Ukraine

Remarks.—The strongyles (Fig. 5V–X) may belong to one of the species of *Petrosia* Vosmaer, 1885 (compare *Petrosia davilai* Alcolado, 1979, Silva and Zea 2017: fig. 2) or *Xestospongia* Laubenfels, 1932 (*X. deweerdtae*, Silva and Zea 2017: fig. 5).

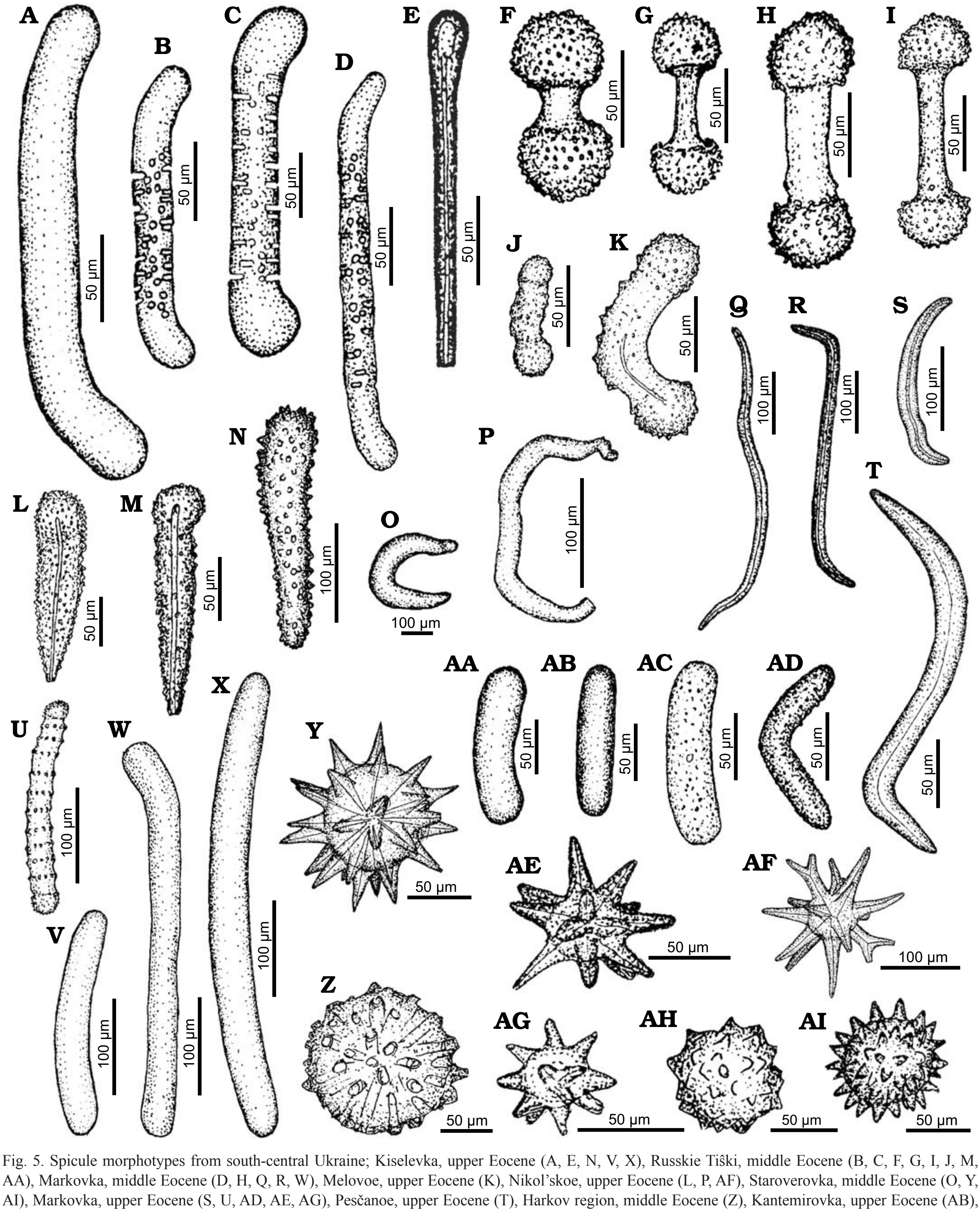

Fig. 5. Spicule morphotypes from south-central Ukraine; Kiselevka, upper Eocene (A, E, N, V, X), Russkie Tiŝki, middle Eocene (B, C, F, G, I, J, M, AA), Markovka, middle Eocene (D, H, Q, R, W), Melovoe, upper Eocene (K), Nikol'skoe, upper Eocene (L, P, AF), Staroverovka, middle Eocene (O, Y, AI), Markovka, upper Eocene (S, U, AD, AE, AG), Pesčanoe, upper Eocene (T), Harkov region, middle Eocene (Z), Kantemirovka, upper Eocene (AB), Russkie Tiŝki, upper Eocene (AC), and Kiselevka, middle Eocene (AH). **A**–**D**, **V**–**X**. Strongyles. **E**. Exotyle. **F**–**K**. Acanthostrongyles. **L**–**N**. Acanthostyles. **O**, **P**. Ophirhabds. **Q**–**T**. Flexuous oxeas. **U**. Acanthostrongyle. **Y**. Oxyspheraster. **Z**. Oxyaster. **AA–AD**. Microstrongyles. **AE**, **AG**. Oxyasters. **AF**. Oxyaster. **AH**, **AI**. Spherasters. After Ivanik (2003); modified.

Order Clionaida Morrow and Cárdenas, 2015

Family Clionaidae d'Orbigny, 1851

Genus *Dotona* Carter, 1880

Type species: *Dotona pulchella* Carter, 1880 (type by monotypy), South India and Sri Lanka.

Dotona sp.

Fig. 5U.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The verticillate cylindrical acanthostrongyle (Ivanik 2003: pls. 18: 5, 19: 1; Fig. 5U) covered with spirally coiled rows of tubercles and with microspined heads can be found in the modern clionaid *Dotona pulchella* Carter, 1880 (compare Calcinai et al. 2001: fig. 2a, b). However, the spicules of *Dotona* do not exceed 100 µm in length, while the spicules described by Ivanik (2003) are twice as long (200 µm). This type of spicules resembles also acanthostrongyles of acarnid *Zyzzya* (compare *Z. fuliginosa* [Carter, 1879], van Soest et al. 1994: figs. 19, 20).

Family Placospongiidae Gray, 1867

Genus *Placospongia* Gray, 1867

Type species: *Placospongia melobesioides* Gray, 1867 (by original designation), geounit Palawan/North Borneo, Recent.

Placospongia spp.

Fig. 1D, F.

Material.—Middle Eocene, south-central Ukraine

Remarks.—The bean-shaped to round, massive, 70–85 µm long microsclere spicules with polygonal plates between the grooves arranged on the spicule surface (Fig. 1D, F) are selenasters. This type of spicules is characteristic for clionaid genus *Placospongia*.

The nearly spherical spicule (Fig. 5AH) might also belong to this genus, except that it is considerably bigger than the spherasters typically found in *Placospongia*. As such, this assignment should be treated with caution.

Family Spirastrellidae Ridley and Dendy, 1886

Spirastrellidae indet.

Fig. 6X.

Material.—Middle Eocene, south-central Ukraine.

Remarks.—The anthasters (Fig. 6X); that is, spherasters with complex ray tips, are similar to the spicules characterizing modern spirastrellid *Diplastrella megastellata* Hechtel, 1965 (compare Rützler et al. 2014: fig. 19b).

Order Polymastida Morrow and Cárdenas, 2015

Family Polymastiidae Gray, 1867

Genus *Sphaerotylus* Topsent, 1898

Type species: *Polymastia capitatus* Vosmaer, 1885 (by original designation), geounit Northern Norway and Finnmark, Recent.

Sphaerotylus spp.

Fig. 6A–C.

Material.—Middle Eocene, middle-upper Eocene, south-central Ukraine.

Remarks.—The club-shaped spicules (Fig. 6A, B) resemble exotyles of Recent *Sphaerotylus*, especially those of *S. vanhoeffeni* Hentschel, 1914 (Plotkin et al. 2017: fig. 29d). Also, the tylostyles (Fig. 6C, ?D) and a fragment of the club-shaped spicule (Fig. 6G) could be part of an exotyle and assigned to one of the *Sphaerotylus* species (compare Plotkin et al. 2017: fig. 18).

Order Poecilosclerida Topsent, 1928

Family Mycalidae Lundbeck, 1905

Genus *Mycale* Gray, 1867

Type species: *Hymeniacidon lingua* Bowerbank, 1866 (by subsequent designation; Thiele 1903), Celtic Seas, Recent.

Mycale spp.

Fig. 6H.

Material.—Middle Eocene, south-central Ukraine.

Remarks.—The nail-shaped spicule (Fig. 6H), even if incomplete and lacking a central button on its top, strongly resembles those of modern *Mycale* (*Rhaphidotheca*) *loricata* (Topsent, 1896) (compare van Soest and Hajdu 2002: fig. 13a, b). A club-like spicule (Fig. 6G) is similar to those in *Mycale* (*R.*) *arctica* Fristedt, 1887 (compare Koltun 1959: pl. 70: 25) and could be attributed to *Mycale* as well.

Family Coelosphaeridae Dendy, 1922

Genus *Histodermella* Lundbeck, 1910

Type species: *Histodermella ingolfi* Lundbeck, 1910 (by subsequent designation; Laubenfels 1936), South and West Iceland, Recent.

Histodermella spp.

Fig. 6N, O, Y, Z.

Material.—Middle Eocene, middle-upper Eocene, south-central Ukraine.

Remarks.—The long oxeas that are spined along their whole length except for their tips (Ivanik 2003: pls. 20: 8, 9, 21: 1; Fig. 6N, O) could probably be assigned to *Histodermella*. This genus includes 4 extant species (van Soest et al. 2018). Three of those species (*Histodermella kagigunensis* Lehnert, Stone, and Heimler, 2013, *H. natalenisis* [Kirkpatrick, 1903], and *H. inglofi* Lundbeck, 1910) possess this type of spicules (compare Kirkpatrick 1903: pl. 6: 18; Lehrnert et al. 2013: fig. 1; Lundbeck 1910: pl. 4: 4).

In addition, the fusiform tylotes (Fig. 6Y, Z) can be found in *H. natalensis* as well (compare Kirkpatrick 1903: pl. 7: 18a). However, a coelosphaerid or myxillid (see below) affinity of that spicule (compare *Coelosphaera* [*Coelosphaera*] *tubifex* Thomson, 1873, Boury-Esnault et al. 1994: fig. 80a) cannot be ruled out either but is less possible.

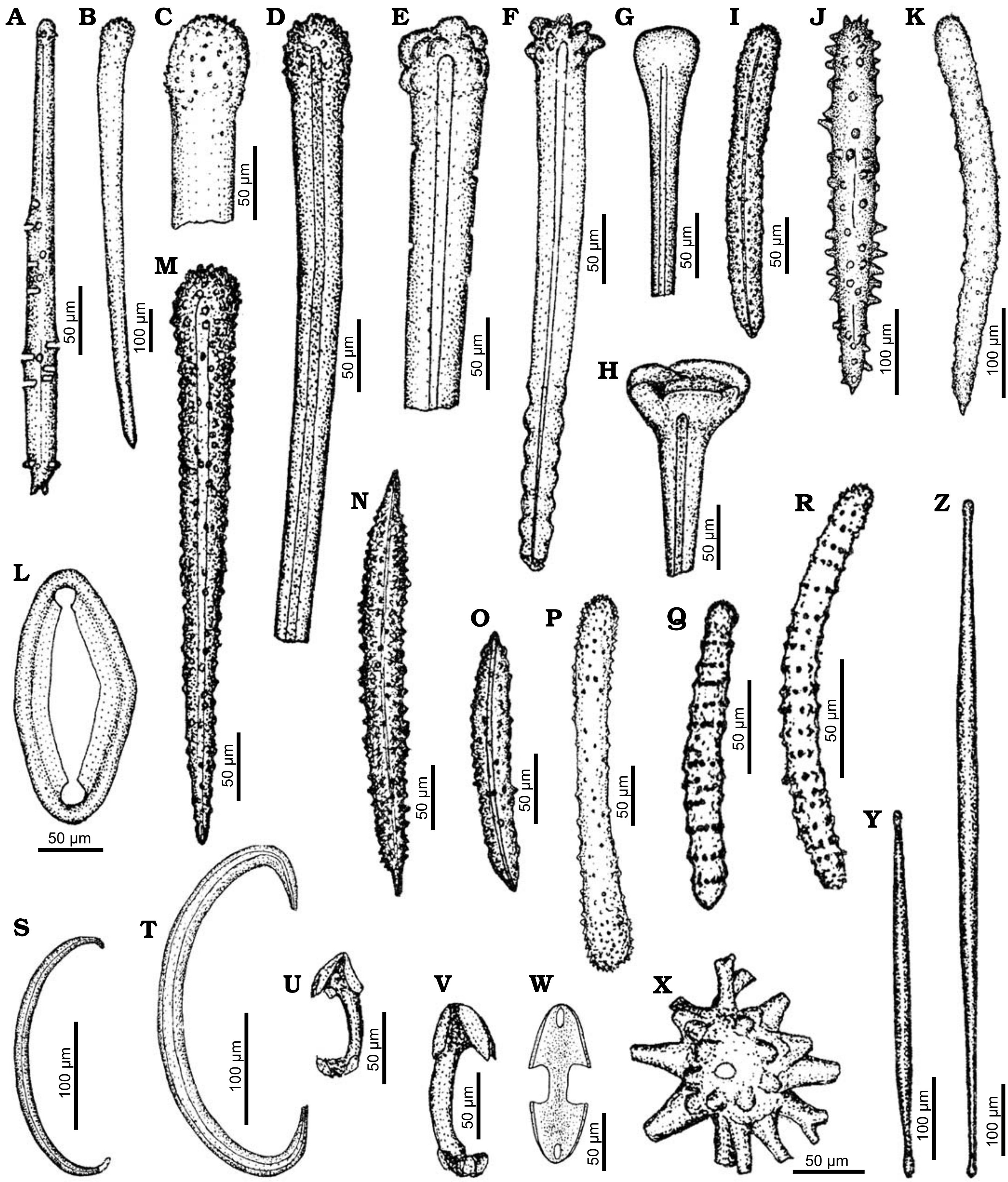

Fig. 6. Spicule morphotypes from south-central Ukraine; Russkie Tiŝki, Middle Eocene (A, H, O, Y, Z), Kiselevka, upper Eocene (B, C), Markovka, middle Eocene (D), Russkie Tiŝki, upper Eocene (E), Kiselevka, upper Eocene (F, G, M), Pogonovka borehole, upper Eocene (I), Markovka, upper Eocene (J, K, N), Nikol'skoe, upper Eocene (L, P), Grigorevka borehole, upper Eocene (Q, R, S, T), Melovoe, upper Eocene (U, V), and Kiselevka, middle Eocene (W, X). **A**. Spherostyle. **B**–**D**. Tylostyles. **E**, **F**, **I**–**K**, **M**. Acanthostyles. **G**, **H**. Exotyles. **L**. Clavidisc. **N**, **O**. Acanthoxeas. **P**–**R**. Acanthostrongyles. **S**, **T**. Sigmas. **U**, **V**. Anisochelae. **W**. Isochela. **X**. Spheraster. **Y**, **Z**. Tylotes. After Ivanik (2003); modified.

Family Myxillidae Dendy, 1922

Genus *Myxilla* Schmidt, 1862

Type species: *Myxilla* (*Myxilla*) *rosacea* (Lieberkühn, 1859), Adriatic Sea, Recent.

Myxilla spp.

Fig. 6I, K, U, V.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—Several spicules of different morphology may be assigned to the family Myxillidae, or even to the genus *Myxilla*. These are the acanthostyles (Fig. 6I, K), and anisochelae (Fig. 6U, V). However, this attribution is not unambiguous and their referral to mycalids is also possible. Still, the slender fusiform tylotes (Fig. 6Y, Z), that were here ascribed to *Histodermella*, might be also of myxillid affinity.

Family Microcionidae Carter, 1875

Microcionidae indet.

Fig. 6E, F, J, M.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The acanthostyles with massively sculptured heads (Fig. 6E, F), as well as other acanthostyles illustrated on the same figure (Fig. 6J, M), could be assigned to some of the microcionid genera. For instance, the former resemble the acanthostyles present in modern *Clathria* (*Thalysias*) *zeai* van Soest, 2017 (compare van Soest 2017: fig. 95b, e). Similar spicules also appear in *Discorhabdella* Dendy, 1924 (compare Boury-Esnault et al. 1994: fig. 83a).

Order Merliida Vacelet, 1979

Family Merliidae Kirkpatrick, 1908

Genus *Merlia* Kirkpatrick, 1908

Type species: *Merlia normani* Kirkpatrick, 1908 (type by original designation), Azores, Canaries, Madeira, Recent.

Merlia sp.

Fig. 6L.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The small oval, ring-shaped spicule called clavidisc shown on Fig. 6L can be assigned to one of the species of *Merlia*. Four recent species of *Merlia* are distinguished and three of them, *M. normani* Kirkpatrick, 1908, *M. tenuis* Hoshino, 1990, and *M. deficiens* Vacelet, 1980, possess clavidiscs. The spicule that is illustrated here can be assigned to one of these species or its close relatives. It is worth noting that *Merlia* is characterized by basal calcareous skeleton that was not found in these deposits. Similar calvidiscs, not associated with basal calcareous skeleton, are known since the Early Jurassic (Wiedenmayer 1994).

Family Acarnidae Dendy, 1922

Genus *Zyzzya* Laubenfels, 1936

Type species: *Zyzzya fuliginosa* (Carter, 1879) (type by original designation), Torres Strait Northern Great Barrier Reef, Recent.

Zyzzya sp.

Fig. 6P–R.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The verticillate acanthostrogyles (Fig. 6Q, R) and acanthostrongyle (Fig. 6P) can be assigned to one of the species of *Zyzzya*. Five species are currently distinguished within this genus (van Soest et al. 2018). Amongst them, *Z. fuliginosa* (Carter, 1879) is characterized by presence of both these spicule types (compare van Soest et al. 1994: figs. 19, 20). The length of the acanthostrongyles found in modern *Z. fuliginosa* is up to 250 μm (see van Soest et al. 1994: table 2), while the fossil spicule is 165 μm long, thus falling within the range observable in that taxon. There are also some other spicules of similar morphology (Fig. 5U). However, contrary to the verticillate acanthostrongyles of *Zyzzya*, these spicules are strongly sculptured also at the tips. Such morphology makes their attribution to Acarnidae less likely.

Family Crellidae Dendy, 1922

Crellidae indet.

Fig. 4S.

Material.—Upper Eocene, south-central Ukraine.

Remarks.—The long acanthorhabd with slightly spirally twisted rhabd and long spines along the whole spicule (Fig. 4S) may belong to some sponges of the family Crellidae. Today, there is a single species known in this family, *Crellastrina alecto* which is characterized by similar, though smaller (up to 120 μm long), curved acanthoxeas (compare Topsent 1904: pl. 15: 16). Besides, the acanthoxeas present in this species are characterized by rugose spine tips which distinguishes them from the fossil spicules described by Ivanik (2003). Thus, the fossil spicule that is illustrated here may belong to unknown species of *Crellastrina*.

Other demosponge spicules

Material.—Lower Eocene, middle–upper Eocene, upper Eocene, Upper Cretaceous, south-central Ukraine.

Remarks.—The long bent oxeas (Fig. 2N, O) might belong to sponges of the suborder Astrophorina.

Pinakid spicules (Fig. 2W–Y); that is, flat oval discs with peripherally arranged gaps (that can be marginally open), are difficult to assign to a family level taxon as no such spicules are known in living sponges. They probably belong to some demosponges related to the geodiid *Erylus*, e.g., *E. monticularis* Kirkpatrick, 1900. This species possesses aspidasters that resemble the pinakids. Pinakids are quite common in the fossil record (Carter 1871; Mostler 1986: fig. 35.12–15, Schrammen 1924: pl. 7.43).

Some of the spicules illustrated by Ivanik (2003), such as those on Fig. 5O, P, resemble ophirhabds present in bubarid

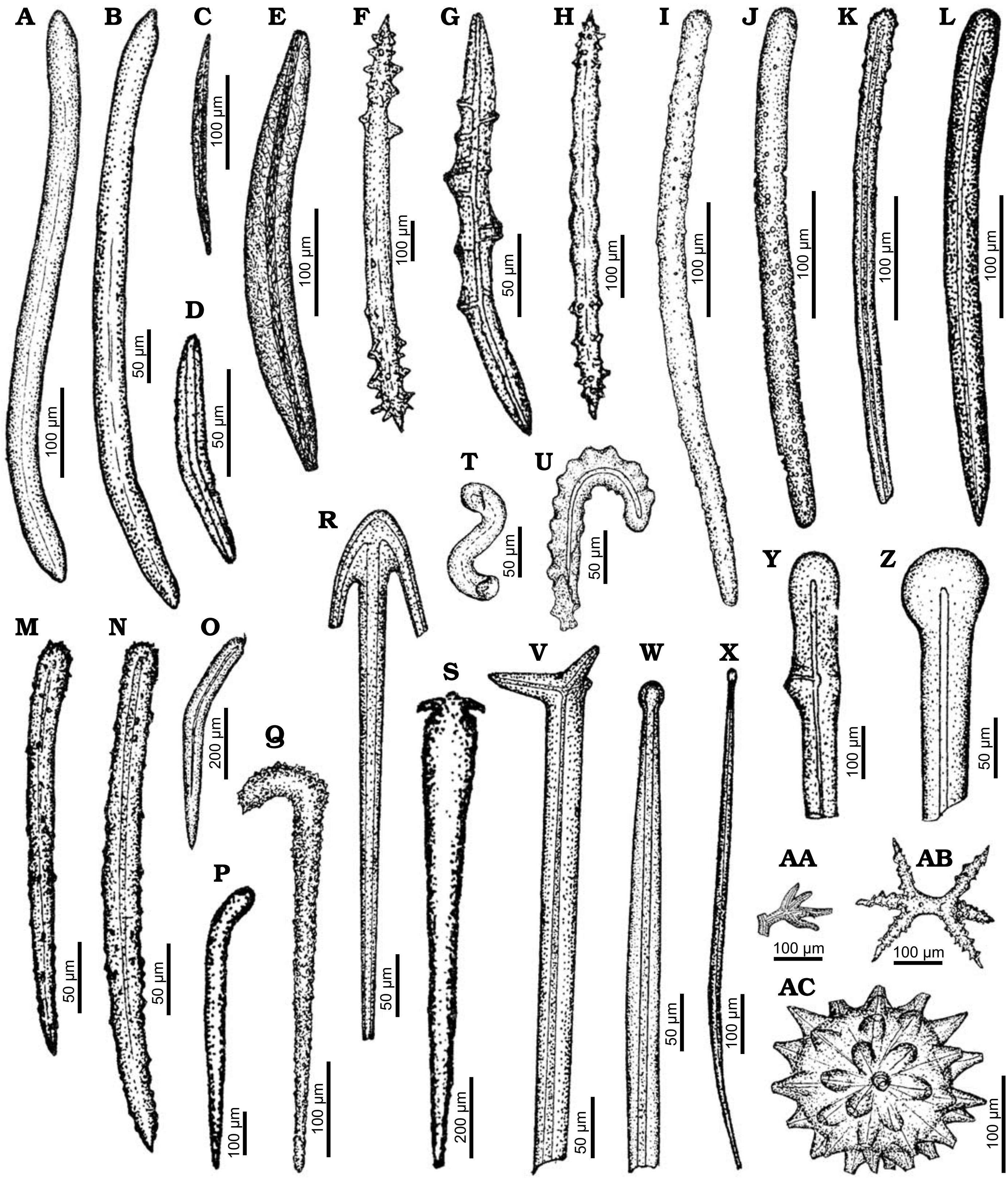

Fig. 7. Spicule morphotypes from south-central Ukraine; Markovka, upper Eocene (A, E, K), Kiselevka, middle Eocene (B, U), Lipcy, middle Eocene (C), Russkie Tiŝki, middle Eocene (D, J, P, R, V, W, X, AB), Nikol'skoe, upper Eocene (F, H, Y), Kantemirovka, upper Eocene (G, L, AA), Kiselevka, upper Eocene (I, O, Z), Pogonovka, upper Eocene (M, N), Melovoe, upper Eocene (Q, T), Černoleska, upper Eocene (S), and Staroverovka, middle Eocene (AC). **A–E**. Oxeas. **F**, **H**. Acanthoxeas. **G**. Acanthorhabd. **I**, **J**. Acanthostrongyles. **K**, **M**, **N**. Acanthostyles. **L**, **O–Q**. Styles. **R**. Reduced triaene. **S**. Anatriaene. **T**, **U**. Unknowns spicule. **V**. Orthotriaene. **W**, **X**. Tylostyles. **Y**. Spicule fragment. **Z**. Exotyle. **AA**. ?Fragment of a triaene. **AB**. Amphiaster. **AC**. Spheraster. After Ivanik (2003); modified.

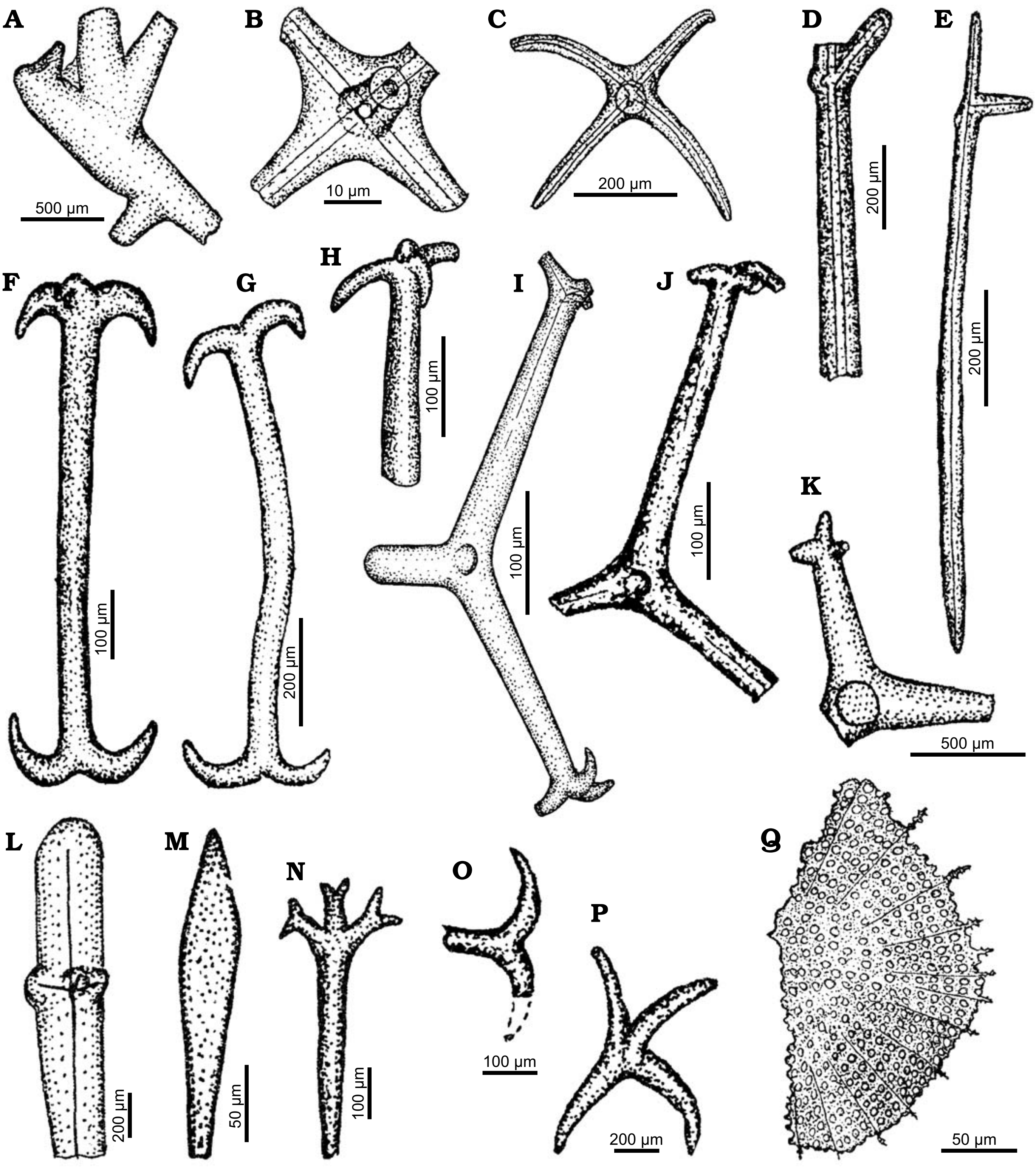

Fig. 8. Spicule morphotypes from south-central Ukraine; Verhnee, lower Eocene (A, K, L, P), Russkie Tiŝki, middle Eocene (B, D, N, Q), Nikol'skoe, upper Eocene (C, E, G, J), Markovka, upper Eocene (F, O), Lipcy, middle Eocene (H), Melovoe, upper Eocene (I), and Kantemirovka, upper Eocene (M). **A**. ?Fragment of dictional skeleton. **B**. Pentactine. **C**. Hexactine. **D**, **E**. ?Oxeas. **F**, **G**, **O**. Amphiclads. **H**. Broken lophodiactine. **I**, **J**. Lophocalthrops. **K**. ?Lophocalthrop. **L**. Spicule fragment. **M**. ?Spicule fragment. **N**. Dichotriaene. **P**. Calthrop. **Q**. Fragment of a diatom. After Ivanik (2003); modified.

sponges. However, the general morphology of these spicules make their assignment difficult.

The desma illustrated on Fig. 9L is also difficult to be attributed to a taxon with certainty. Still, its morphology resembles the triders of Phymaraphinidae. The lithistid ectosomal irregular phyllo/dichotriaene (Fig. 9C) cannot be

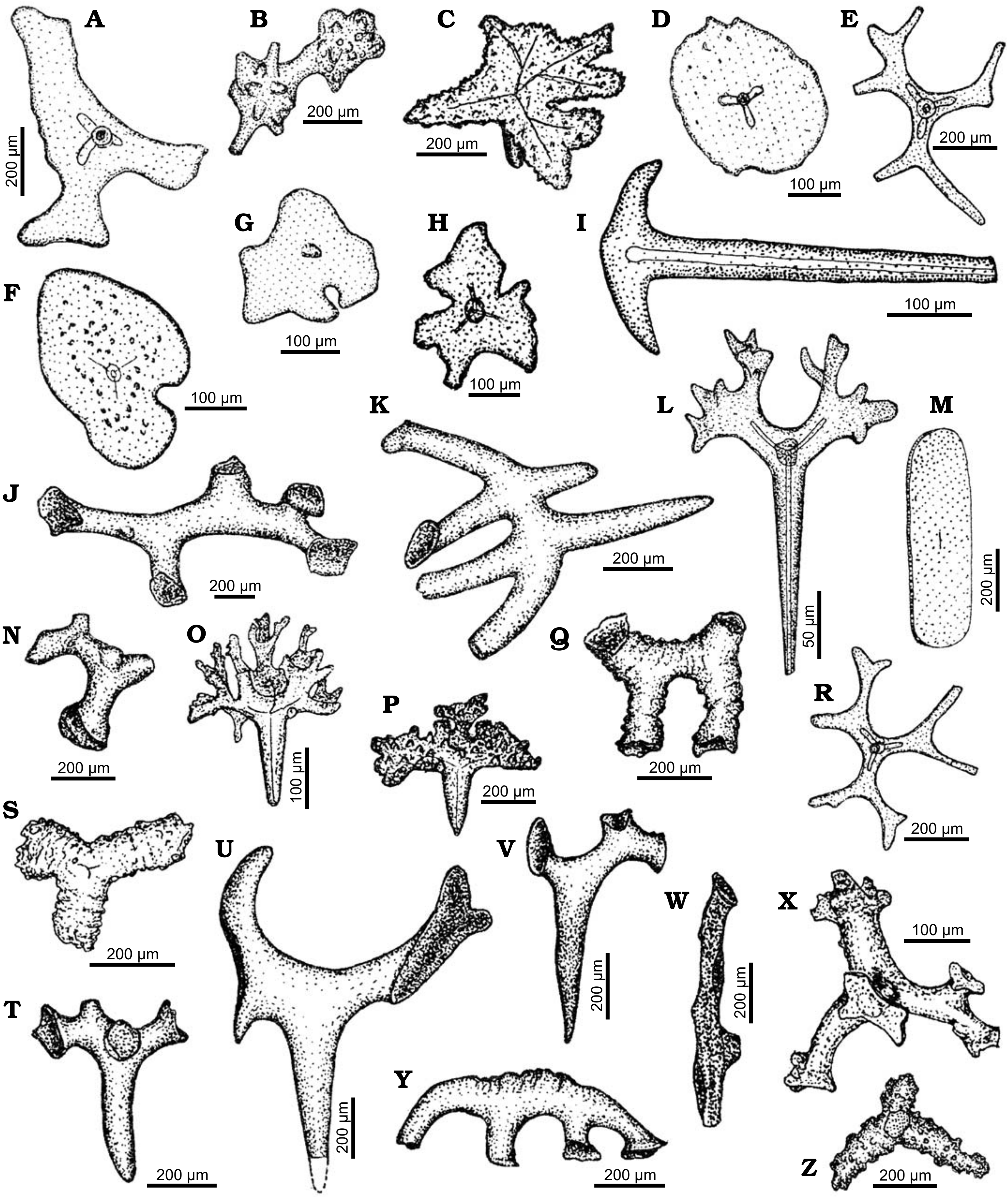

Fig. 9. Spicule morphotypes from south-central Ukraine (A–V, X–Z) and Lithuania (W); Markovka, middle Eocene (A, D, E), Verhnee, lower Eocene (B, Z), Glâdov Âr, Upper Creatceous (C, J, K, P, Q, T, U, V, Y), Pesčanoe, upper Eocene (F, O), Kiselevka, middle Eocene (G, L, R), Markovka, upper Eocene (H, X), Nikol'skoe, upper Eocene (I, S), Lipcy, middle Eocene (M), Monastyrek, lower Eocene (N), and Neravai borehole, Paleocene (W). **A**, **C**, **E**, **H**, **L**, **O**, **P**, **R**. Phyllotriaenes. **B**. Sphaeroclone. **D**, **F**, **G**. Discotriaenes. **I**. Anchorate spicule. **J**, **K**, **N**, **Q**, **S**–**W**, **Y**. Megaclones. **M**. Siliceous plate. **X**, **Z**. Tetracrepid desmas. After Ivanik (2003); modified.

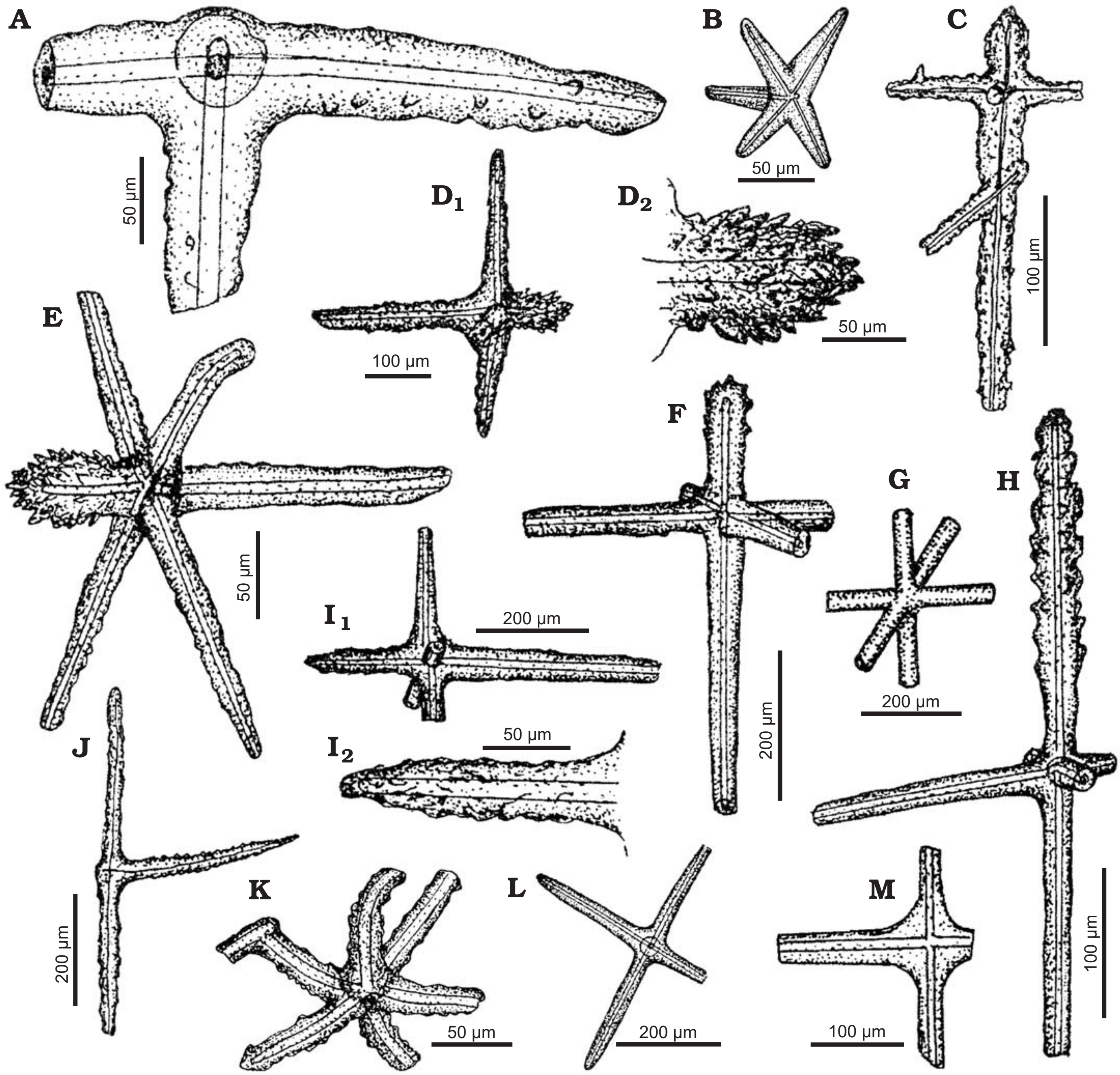

Fig. 10. Spicule morphotypes from south-central Ukraine; Kiselevka, middle Eocene (A, F, H, I, L), Staroverovka, middle Eocene (B), Nikol'skoe, upper Eocene (C, D, E, J, M), Russkie Tiŝki, upper Eocene (G), and Russkie Tiŝki, middle Eocene (K). **A**, **B**. Pentactines. **C**–**F**, **H**, **I**. Pinnular hexactines. **G**. **S**mooth hexactine. **J**. Tautactine. **K**, **L**, Hexactines. **M**. Stauractine. After Ivanik (2003); modified.

easily attributed to any lower taxon as well. On the contrary, the object (Fig. 8Q) illustrated by Ivanik (2003), attributed by him to the category of discoidal spicules, is actually a fragment of a diatom.

Class Homoscleromorpha Bergquist, 1978

Order Homosclerophorida Dendy, 1905

Family Plakinidae Schulze, 1880

Genus *Placinolopha* Topsent, 1897

Type species: *Placinolopha bedoti* Topsent, 1897 (by original designation), Banda Sea, Recent.

Placinolopha spp.

Fig. 8F–K, O.

Material.—Lower, middle, upper Eocene, south-central Ukraine.

Remarks.—Many spicules display features characteristic for the sponges of the smallest modern sponge class, Homoscleromorpha. They are characterized by the lophate actine tips. There are several 500–600 μm long lophodiactines (Fig. 8F–H, O) that resemble amphiclads of the Recent species *Placinolopha sarai* Lévi and Lévi, 1989 (compare Lévi and Lévi 1989: fig. 13). In turn, some lophoclathrops (Fig. 8I, J, possibly K) with long lophate clads characterize modern *Placinolopha moncharmonti* Sarà, 1960 (compare Sarà 1960: fig. 1).

Class Hexactinellida Schmidt, 1870

Hexactinellida indet.

Figs. 8B–E, 10A, B, D, E–G, I–L.

Material.—Middle, middle–upper Eocene, south-central Ukraine.

Remarks.—The hexactines illustrated on Fig. 10C, E, F, I, H are most probably dermal spicules of rosselid sponges (compare Tabachnick 2002b: figs. 18, 19). However, similar spicules can be found also in other hexactinellid groups, e.g., Euretidae Zittel, 1877 (order Sceptrulophora), Aphrocallistidae Gray, 1867 (order Hexactinosida), or even in the amphidiscosid family Pheronematidae Gray, 1870 (see Reiswig 2002a; Reiswig and Wheeler 2002; Tabachnick and Menshenina 2002b). Yet, their rossellid affinity seems most likely because another spicule illustrated on the same figure (Fig. 10J), called dermal triactine, is also noted in the rossellid sponges (compare Tabachnick 2002b: fig. 40d). Besides, a fragment of the sparsely tuberculated pentactine (Fig. 10A) can be attributed to rossellids as well. It resembles especially the hypodermal pentactines of *Crateromorpha* (*Neopsacas*) Tabachnick, 2002b (see Menshenina et al. 2007: figs. 2k, 7h; as well as Tabachnick 2002b: fig. 18e).

In turn, the hexactine with a rough, weakly tuberous surface, slightly bent rays, and one ray fusing with a fragment of another spicule (Fig. 10K) seems to be a part of dictyonal framework of hexasterophorid sponges (see Reiswig 2002b: figs. 2b, 3c; 2002c: fig. 2b–d; Reiswig and Wheeler 2002: fig. 8B).

Some anchorate basalia (Fig. 10J) may belong to pheronematid sponges (compare Lévi and Lévi 1989: fig. 2).

Some pentactines (Figs. 8B, 10B) and stauractines (Fig. 10M) resemble dermalia of *Symplectella* Dendy, 1924 (Lyssacinosida, Euplectellidae) (see Tabachnick 2002a: fig. 27f–h).

The oxyhexactines (Figs. 8C, 10L) show some affinity to choanosomal spicules of *Hyalonema* Gray, 1832 (Amphidiscosida, Hyalonematidae) (see Tabachnick and Menshenina 2002a: fig. 1l). Amongst the spicules of unquestionable hexactinellid affinity are also those illustrated on Figs. 8B, D, E, 10K, but their more accurate attribution is impossible.

Concluding remarks

A reassessment of the disassociated Paleogene sponge spicules from the southwestern of the East European Platform studied by Ivanik (2003) revealed a diverse sponge fauna. The fauna appears to be dominated by Demospongiae (at least 24 families) while Hexactinellida were relatively rare but diverse. The majority of spicules attributable to hexactinellids appear to be dermal pentactines and their derivatives, most likely representing the family Rossellidae. Potentially, a single genus of Homoscleromorpha was recognized as well.

This reassessment, together with a new as yet unpublished material (MŁ, AP, and TS, unpublished data), will serve as a baseline for further taxonomic, ecological, and biogeographic studies of the poorly known Paleogene sponge fauna of this region.

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