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Paleoanthropology

Hominid Fossils from Dmanisi and Their Place Among the Early Hominids

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ABSTRACT. Discoveries of *Homo* remains consisting of four craniums and four mandibles with several postcranial remains, stone artifacts of Olduvai type Mode 1 (13) and faunal fossils that points to a latest Pliocene – earliest Pleistocene age during the excavations in Dmanisi, Republic of Georgia, yielding the age of 1.81 M. yr. (Ar_{40}/Ar_{39}) have reopened the debate about the first human dispersal out of Africa; being one of the problematic questions for the paleoanthropologists. The Dmanisi paleodeme presents numerous primitive characters, typical to Early African hominids, but it as well shares quite big similarities with *Homo erectus*, and is probably better accommodated to the latter species. Dmanisi, presenting a small-brained population, could have been the ancestors of the African and Far East branches of *H. erectus* having more derived morphology. *© 2007 Bull. Georg. Natl. Acad. Sci.*

Key words: *hominids, H. georgicus, paleodeme, human dispersal, early Pleistocene.*

Introduction

Dmanisi is located in the Lesser Caucasus, Republic of Georgia, 85 km south-west of Tbilisi on the promontory, at the confluence of the Mashavera and Pinezauri rivers. The Early Paleolithic site of Dmanisi was discovered in 1983, under the deserted medieval town of Dmanisi (see Fig.1). The excavations of the ruins of the medieval dwelling started in 1936, but beneath the medieval cellars archaeologists found animal bones, among which, in 1983, paleontologist Prof. A. Vekua identified the tooth of rhinoceros *Dicerorhinus etriscus etruscus*, typical of the Early Pleistocene age. In 1984, the first stone tools were discovered. Since then the site has been excavated until now on. Already in 1991 the first hominid remains – well preserved mandible D211 [1-3] were discovered, followed by two hominid crania – D2280, D2282 [4, 6] and a metatarsal [5] in 1999. After, Dmanisi produced the surprisingly big mandible D2600 [7] in 2000; almost complete subadult skull in 2001 (D2700/D2735) [8], and finally the skull of an edentulous adult (D3444/D3900 – in 2002/2004) [9]. D2282 is now linked with D211 jaw [10]. Dmanisi documents a very early dispersal out of Africa, clarifying that western Asian populations were important in the origin, evolution and expansion of *H. erectus* [11].

Stratigraphy

Radiometric and paleomagnetic data show that all of the Dmanisi fossils were buried shortly after the Olduvai-Matuyama reversal at ca. 1.77 Ma [6, 11]. Dmanisi hominids were deposited and sealed by calcretes in less than 10000 years; this rapid burial is a reason of particularly intact taphonomic condition [11].

The stratigraphy itself is represented by two main units – **A** and **B**, each of these units is divided into sub-

Fig. 1 Medieval town of Dmanisi

units – **A1, A2, B1** and **B2, A-B** contact is an abrupt erosional surface composed of carbonated rock. These layers are deposited over the basaltic lava that constructs the ground relief of the Dmanisi promontory. This lava flow had formed a natural dam to those two rivers (Mashavera and Pinezauri) that gave rise to an ephemeral lake, later causing the appearance of the promontory [6].

Dmanisi Hominids, Taxonomy, and Environment

The first mandible **D211** [14-16] is not complete, because both *rami* are missing, but the corpus is quite well preserved having an **V**-shape, all the 16 teeth are present showing the low wear degree (see Fig.2).

Although the facial part is missing, the braincase of the cranium **D2280** is complete, small in size as all the rest of the Dmanisi hominids with the endocranial capacity of 775 cm^3. This skull with a thickened brow ridge, strong angular torus and deeply incised nuchal lines, could be considered as a male individual [10].

The specimen **D2282** (see Fig. 3) contains much of the face and cranial vault but has undergone lateral and dorso-ventral post-mortem deformation. This individual is smaller with an endocranial capacity of 650 cm^3 to 660 cm^3 with gracile muscle attachment areas, less well-developed

Fig. 2. Mandible D211. Occlusal view

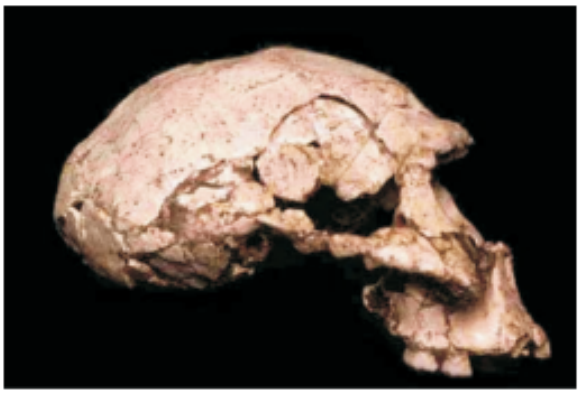

Fig. 3. Cranium D2282. Lateral view

Fig. 4. Mandible D2600. Lateral view

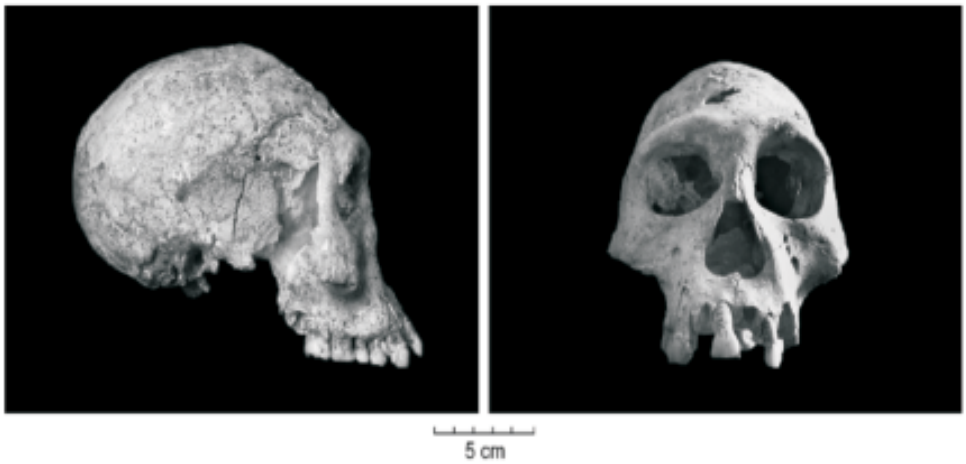

Fig. 5. Cranium D2700. Lateral and facial views

Fig. 6. The edentulous skull D3444/D3900.

cranial supersutures, light dental wear and well demarcated cranial sutures that enables to say that it was either an older subadult or young adult and possibly a female [10].

The mandible **D2600** (see Fig. 4) just overlay the Mashavera basalt. The size of the mandible is unusually big: the whole length is 126.9mm, width – 133.5mm and the height of the ascending ramus is 91mm [12]. The teeth are very worn getting till the roots that are remarkably well-developed. The peculiarity of this mandible is also the double-rooted P3 – characteristic of the Paranthropus and *H. rudolfensis.* The morphological differences and remarkably big sizes, comparing to the rest of the hominids, made some of the scientists propose to separate it as new species - *H. georgicus* [7, 8]. This mandible also shows the M1>M3 size reduction that is not characteristic of any of the other Dmanisi mandibles. D2600 also differs by a significant height of the mandible and unaccustomed structure of the posterior part of symphysis (Table 1), as well as by the existence of the well developed canine crests.

The skull **D2700** (see Fig. 5) with the associated mandible **D2735** is in a remarkably good condition. This speci-

Table 1

Mandibular measurements for Dmanisi hominids

	D2735	D211[a]	D2600
Symphisys height	34	30.8	49
Symphisys thickness	16	16.8	21
Corpus height (M1)	22.5	(24.7)	41
Corpus breadth (M1)	19	18.4	21
Robusticity index (M1)	84.4	74.5	51.2
Cross-sectional area (M1)*	335.7	356.9	676.2

Where damage is appreciable, () indicates that only an estimate is possible.[a] – Dimensions from Gabunia and Vekua (1995) * - Calculated as π (1/2 height) (1/2 breadth)Rightmire et. al. 2005

men is a subadult, with partially erupted M3s. Some of the teeth are found in an isolated way that absolutely well fit the skull. The damage can be observed on the orbital walls and the fragile elements of the interorbital region, anterior part of the maxillarae, as well as can be seen the eroded mastoid process; also zygomatic arches are broken [10]. The cranial capacity is 600cm^3 [8].

The edentulous skull **D3444** with the associated mandible **D3900** (see Fig. 6) with the cranial capacity of 650 cm^3 is clearly an adult, displaying many of the features anticipated in males of the genus *Homo* – the glabellar region is broad and prominent, supraorbital tori are projecting, mastoid crests are strongly developed and the mastoid portion of the temporal bone is laterally inflated; the upper face is relatively broad and the cheeks are massive [11]. The condition of the alveoli proves that this individual had lived several years after losing the teeth; the explanation to this is that the tooth sockets (alveoli) and alveolar arch is absolutely resorbed and atrophied. The hypothesis of the survival of this individual could be utilization of the softer plants, as well as the extraction of the animal brain and marrow with stone tools and manuports, or that the Dmanisi hominids could offer assistance and care [11].

The Morphometric data (Tables 3,4) collected from the Dmanisi homnid skulls showed vivid similarities with the African hominids – *H. erectus.* These hominid remains share the general shape of the cranial morphology, well-developed supraorbital tori, similar frontal and occipital inclination relative to Frankfurt Horizontal [7], relative narrowness of the post-orbital region and moderate height of the cranial vault and the thickness of its bones, also relief of the occipital area. Massive mastoid process and the pneumatization of the mastoid area, morphology of temporomandibular articulation, as well as the narrowness of the alveolar arch, elevated nasal

Table 2

States for characters identified in the Dmanisi crania and mandibles.
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Plesiomorphies for *Homo*

- Low cranial capacity (600 to 775 cm^3)
- Frontal narrowing pronounced (postorbital constriction index 68.7 to 74.4)
- Mastoid region inflated and laterally projecting
- Occipital transverse torus poorly expressed or absent
- Low occipital scale index (85.0 to 102.1)
- Midfacial contour projecting
- Canine jugum prominent and laterally bounded by maxillary sulcus
- Zygomaticoalveolar incisure present
- Hard palate shallow
- Palatal opening to incisive canal situated posteriorly
- Mental eminence slight or absent
- Symphysis buttressed internally (superior transverse torus)

Synapomorphies with *H. erectus* (*sensu lato*)

- Supraorbital torus bar-like and projecting
- Bregmatic eminence with parietal sagittal keel
- Angular torus present
- Temporal squama low with straight upper border
- Mastoid tip inturned and flattened posteriorly
- Low petrotympanic angle (140º to 150º)
- Petrous pyramid smooth ("dense") in appearance
- Foramen lacerum restricted
- Nasal saddle prominent

Possible synapomorphies with Asian *H. erectus*

- Parasagittal flattening (depression) of parietal surfaces
- Paramastoid and occipitomastoid crests present

Possible autapomorphies in the Dmanisi paleodeme

- Double sagittal keel
- Relatively delicate tympanic plate
- Supratubarius process absent
- M3 reduced in size

Table 3

Cranial measurements (mm) for the Dmanisi hominids and selected representatives of earlier Homo

	DMANISI				EARLY HOMO		H. ERECTUS (Africa)			H.ERECTUS (Asia)		
	D2700	D2280	D2282	D3444	ER1813	ER1470	ER3733	ER3883	WT15000	Sangiran 2	Sangiran 4	Sangiran 17
Whole vault												
Cranial length	155	177	–	163	145	168	182	182	–	–	–	207
Basion-nasion length	92	–	–	–	82?	–	107	102	–	–	–	115
Basion-prosthion length	100?	–	–	–	94?	–	118	–	–	–	–	129?
Basion-bregma height	101	–	–	–	98?	–	111?	102	106?	–	–	114?
Max. Cranial breadth	126	136*	–	132	113	>138	142	140	131	141	147	161
Biauricular breadth	119	132*	–	120	112	135?	132	129	–	126	132	140
Frontal bone												
Supraorbital bone thickness												
Central	8	11	10.5	10	9	8	8	11	–	12	–	17
Lateral	6	9	5.5	9	6.5	6.5	9	7	–	8	–	13
Min. Frontal breadth	67	75	66	67.5	65	71	83	80	73	82	–	95
Max. Frontal breadth	85?	105	87?	91?	–	92	110	105	–	102	–	119
Biorbital chord	90	105?	96?	98	91	109	109	110	96	–	–	115
Postorbital constriction index #	74.4	71.4	68.7	68.8	71.4	65.1	76.1	72.7	76	–	–	82.6
Frontal sag. chord	89	101	–	93	80	93	104	101	–	–	–	118?
Frontal sag. Arc	95	108	>95	101	90	104	119	118	–	–	–	–
Frontal angle	150	149	–	148	139	140	139	140	–	–	–	–
Parietotemporal region												
Max. Biparietal breadth	117	119	116?	122	100?	120	131	134	128?	137	140	142
Parietal sag. chord	87	91	82	98	74?	84	82	90	93	98?	–	108?
Parietal sag. arc	91	96	85	105	77?	89	85	95	107	103?	–	–
Lambda-asterion chord	65	70	68	71	64	80	81	74	63	82?	80?	74
Lambda-asterion arc	70	75	72	74	69	88	88	79	76	92?	87?	–
Occipital bone												
Biasterionic breadth	105	104	103?	104	93?	108?	119	115	106	122	126?	124
Occipital sag. chord	70?	76?	–	79	78?	86?	88	75?	69	>71	82	81?
Occipital sag. arc	87?	97?	–	95	96?	105?	118	101?	93	–	108	–
Occipital angle	115.6	108?	–	117	114?	–	103	101	–	–	105	100
Lambda-inion chord	45?	46?	46?	50	55?	60?	57	48	38	45?	47	52
Inion-opisthion chord	39?	47?	–	42.5	40?	45?	53	51	50	45?	56	57
Occipital scale index ^	86.6	102.1	–	85	72.7?	75.0?	92.9	106.2	131.5	100.0?	119.1	109.6
Foramen magnum length	30	–	–	–	–	–	37	33	36	–	40?	39
Foramen magnum breadth	28?	–	–	28	–	–	32?	26?	27	–	31	29?
Foramen magnum area ~	660?	–	–	–	–	–	930?	674?	763	–	974?	888?

* - Obtained by doubling the measurement to the midline; # - Calculated as the ratio of min. frontal breadth to the orbital chord ^ - Calculated as the ratio of the inion-opisthion chord to the lambda-inion chord; ~ - Calculated as ì (1/2 length) (1/2 breadth) Lordkipanidze et. al. 2006

saddle, sagittal keeling on the parietals, a low temporal squama with a straight upper border passing downward toward asterion, flexion of the occiput and a constricted foramen lacerum. But Dmanisi hominids differ from several specimens of Asian *H. erectus* with lesser thickness of the cranial vault bones, more moderately developed supraorbital and nuchal tori and narrower alveolar arches, these specimens are – Trinil and Sangiran 2 from Indonesia. By the small cranial capacity, facial morphology (midfacial projection) and mandibular characteristics (**V**-shape), Dmanisi hominids get close to the Early African homos like *H. habilis* [17-19] and *H. rudolfensis*, despite this they distinguish from African homos by having the angulation of the cranial vault, absence of cresting, large orbital areas and single-rooted maxillary premolars. The other primitive traits showed in Dmanisi paleodeme are flexion of the malar pillar, frontal constriction, inflation of the mastoid region, weak expres-

Table 4

Facial measurements (mm) for the Dmanisi hominids and selected representatives of earlier Homo

	DMANISI			EARLY HOMO			HOMO ERECTUS		
	D2700	D2282	D3444	ER1813	ER1470	ER3733	ER3883	WT15000	Sangiran 17
Nasion-prosthion length	69?	–	–	64	90?	81	–	77?	>75
Biorbital chord	90	96?	98	91?	109	109	110	103	144?
Nasion angle	136	–	142	153	151	155	151	138	141?
Nasal bridge width	18?	–	21	–	–	22	22	32	24?
Nasal bridge height	9	–	9	–	–	8	9.0?	9.5	9.0?
Nasal bridge index *	50	–	42.8	–	–	36.3	40.9	29.6	37.5
Nasal bridge angle	90	–	98	–	–	108	101	119	106
Orbit breadth	35	–	38	34	41?	44?	45	39?	44
Orbit height	31	–	32	30	36?	35	36	42?	40
Midorbital chord	55	–	51	60	64?	73	–	70	66?
Naso-orbital angle	129	–	130	–	136?	135	–	123	123
Nasal breadth	28	27	28	24	27	36?	–	36	29
Nasal height	50	–	50	44	58?	53	–	57	52?
Clivus length	>20	28	–	24?	36?	30?	–	22	25?
Bimaxillary chord	97?	91#	93	86?	98?	101	–	100	116?
Subspinale angle	143?	154?	140	144?	161?	143	–	133	125?
Prosthion angle	107?	107?	–	108?	112?	102	–	103	–
Cheek height	28	30?	25?	27	40?	34	–	30	37
Max. Malar height	39	43.5?	40	–	–	53?	>58	53?	57?
Palate breadth	37?	39	–	35?	–	–	–	40	–
Palate length	55?	54	–	54?	–	–	–	–	–

* - Calculated as the ratio of nasal bridge height to nasal bridge width. # - Obtained by doubling the measurement to the midline Lordkipanidze et. al. 2006.

sion of the occipital transverse torus, a shallow palate, a thickened vertical mandibular symphysis and no (or light) mental eminence, a sloping alveolar planum and internal transverse tori [11].

We can also observe that Dmanisi hominids share some traits only with the far Eastern populations like Ngandong assemblage from Java [11], these synapomorphies are – parasagittal flattening of the posterior vault, as well as the existence of the paramastoid and occipitomastoid crests (Table 2). Some of the traits are autapomorphic for some of the Dmanisi hominids (D3444, D2280), like double sagittal keel, relatively delicate tympanic palate, and the architecture of the medial glenoid fossa [11].

If we foresee the geological age of the Dmanisi hominids, we should presume a high speed of migration. As it turns out, the representatives of *H. erectus* group quite easily managed to leave the tropical zone and through the Levantine corridor invaded the environs of the temperate climate. The paleobotanical and paleontological studies show that mosaic landscape must have prevailed on the territory of Dmanisi, where there were open areas, and nearby the riversides forests were spread. In Dmanisi vertebrate fauna steppe and savannah type landscape habitats mainly predominate pointing to latest Pliocene earliest Pleistocene age, like *Struthio dmanisiensis, Ochotona cf. lagreli, Meriones, Equus stenonis, Giraffa, Gazella borbonica;* Many deer remains that are found at the site is a proof of the existence of a wooded area; the rest of the forest representatives are – *Sorex, Ursus etruscus, Martes sp., and Cervus perrieri* [20]. Biogeographic studies showed that Dmanisi fauna was composed of different bioprovince elements, obviously South Caucasus being a link between African and Eurasian bioprovinces.

The lithic artifacts discovered in Dmanisi (flakes, cores, chopper-choppings etc.) are made of the local sources from the nearby river gravels, using an Olduvan (Mode 1) [13] technology. No bifaces or developed Olduvan artifacts have been found, nor have refits of flakes on tools been found. The Dmanisi assemblage is well-matched with pre-Acheulian assemblages of East Africa, nullifying the previous theories of hominid dispersal – connected with technological progress that caused the mastering of Acheulian technique, after which the hominid migration started.

Conclusion

In summary, we can conclude that the hominid from Dmanisi must have been a small-brained species, with a narrow and highly inclined forehead, moderately developed supraorbital arch, distinctive midfacial prognatism, comparatively narrow nose and alveolar arch, and remarkably small cranial capacity. These hominids are close to a stem, from which other allopatric groups of *H. erectus* are derived. The data is unfailing evidence of viewing the Dmanisi paleodeme as ancestral to African and Far Eastern branches of the species [10]. The Dmanisi find can suggest movement of population from Africa through the Levantine corridor to the Caucasus and finally to southern Asia and the Far East.

პალეოანთროპოლოგია

დმანისელი ნამარხი ადამიანი და მისი ადგილი ადრეულ ჰომინიდებს შორის

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უძველესი ჰომინიდების წარმოშობისა და ევრაზიაში გავრცელების პრობლემა, მათი მიგრაციის გზების დადგენა პალეოანთროპოლოგიის ერთ-ერთი ურთულესი პრობლემათაგანია. მეცნიერებაში აღიარებული ჰიპოთეზის მიხედვით, ჩვენი ბიოლოგიური წინაპარი – პირველი *ჰომო* წარმოიშვა აფრიკაში დაახლოებით 2.5 მლნ. წლის წინ, დიდი ხნის მანძილზე იქვე ბინადრობდა და დაახლოებით 1 მლნ. წლის წინ გავრცელდა ევრაზიაში. დმანისის პალეოანთროპოლოგიურმა აღმოჩენებმა არსებითად შეცვალა ჰიპოთეზა და ახლებურად დააყენა პრობლემა ადრეული ადამიანის ევოლუციის,გავრცელების დროისა და გზების შესახებ. დღეს დავას არ იწვევს ის ფაქტი, რომ ევრაზიაში პირველი ჰომინიდი 1.81 მლნ. წლის წინ (Ar_{40}/Ar_{39}) უკვე ბინადრობდა სამხრეთ საქართველოს ტერიტორიაზე.

დღეისათვის დმანისის ადგილსაპოვებელ'ში აღმოჩენილია ოთხი თავის ქალა, ოთხი ქვედა ყბა, თორმეტი იზოლირებული კბილი და პოსტკრანიალური ჩონჩხის 49 ნაშთი, გადაშენებულ ცხოველთა ათასობით ძვალი, ოლდუვაის ტიპის (Mode I) [13] ქვის იარაღები და ნამარხი მცენარეული ნაშთები. ამ მრავალფეროვანი მასალის შესწავლის შედეგად მეცნიერთა ჯგუფმა დაადგინა პირველი ევროპელი ჰომინიდის მორფოლოგიური ნიშნები, მისი მატერიალური კულტურის თავისებურებები და აღადგინა სავარაუდო საარსებო პირობები [14].

დმანისში აღმოჩენილი თავის ქალების მორფოლოგიური შესწავლის შედეგად დადგინდა, რომ დმანისელი ადამიანი აშკარა მსგავსებას ამჟღავნებს აფრიკულ ჰომინიდებთან, რომელთაც ***Homo erectus***-ს აკუთვნებენ. მსგავსი აქვთ დმანისელ და აფრიკის ადრეულ ჰომინიდებს შედარებით მცირე ზომის თავის ქალა, საერთო ფორმა, შუბლის დაქანება, **V**-ს ფორმის ქვედა ყბა და სხვ. ამავე დროს დმანისელი ჰომინიდი განსხვავდება აფრიკის *H. erectus*-ისაგან თავის ტვინის რამდენადმე უფრო მცირე მოცულობით (*H. erectus*-ის ტვინის მოცულობაა 900 სმ³, ხოლო დმანისის ჰომინიდისა – 600-700 სმ³), ლამბდას მიდამოებში დამატებითი ძვლის არსებობით, მოლარებზე კარაბელის ბორცვის არსებობით და სხვ. [21, 23].

განსაკუთრებით საინტერესოა 2000 წელს აღმოჩენილი ქვედა ყბა (D2600), რომელიც ზომითა და მორფოლოგიური ნიშნებით არსებითად განსხვავდება არა მარტო დმანისში ნაპოვნი ქვედა ყბებისაგან, არამედ საერთოდ დღემდე აღმოჩენილი ადრეული ჰომინიდების ქვედა ყბებისაგან.

ახალი ქვედა ყბის დიდი ზომები, ნაკლები მასიურობა, მკვეთრი ეშვის ქედების არსებობა, ორფესვიანი პირველი პრემოლარები, კბილების პროპორციები (მოლარების ზომების ზრდა M1<M2<M3) საფუძვლად დაედო ახალი სახეობის *H. georgicus-ის* გამოყოფას [7, 8].

დმანისის ნამარხი ფაუნისა და პალეობოტანიკური მასალის შესწავლის შედეგად დადგინდა, რომ დმანისელი ადამიანის მიერ სამხრეთ საქართველოს ტერიტორიის საცხოვრებლად ათვისების პერიოდში იქ მოზაიკური ლანდშაფტი უნდა ყოფილიყო გაბატონებული,სადაც გაშლილი სივრცეების გვერდით წყალგამყოფებზე და მდინარეების ჭალებში ტყით დაფარული უბნებიც იყო წარმოდგენილი.

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